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CHARACTERISTICS OF THE VEGETATION IN CERTAIN TEMPERATE REGIONS OF EASTERN MEXICO [1]

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INTRODUCTION

Much of Mexico has a temperate climate and even though a large portion of its vegetation is distinctly tropical in origin and appearance, a considerable number of species in its flora seem to have had a northern evolution and relationship. This is particularly true of the dominant species (mostly oak and pine) in most of the forests between 3,500 and 6,500 feet. In eastern Mexico certain portions of this temperate vegetation are different from the major part in the composition of the flora and in the unusual structure of the communities which contain a surprising mixture of species with very diverse geographical affinities.

Some of these communities exist in the transition zone (generally situated between 3,300 and 4,000 feet in elevation) between "tierra caliente" (hot country) and "tierra templada" (temperate country). This zone, while easily recognizable, is not as definitely characterized by certain species or communities as are the zones immediately above and below it. A remarkable intermingling of elements of diverse affinities is manifest in regard to communities as well as to individual entities. It should be noted that this transition zone forms the dividing line between elements of the great arcto-tertiary and neo-tropical floristic regions of classical phytogeography.

These eastern areas of Mexico are ecologically unusually interesting for several additional reasons. Growing in them are many species (perhaps also communities or associations) which are decidedly vicariads in relation to the plants of eastern United States. The floristic dissimilarity which exists between eastern and western United States appears to extend into Mexico, but with diminished intensity. There are species of *Alnus, Quercus* and *Pinus* whose relationships are with the flora of western United States growing in the communities of eastern Mexico along with the species of *Liquidambar, Nyssa, Carpinus, Ostrya* and other genera whose affinities distinctly lie with plants in the vegetation of eastern United States. Also in eastern Mexico there are additional species with typically discontinuous ranges which belong to elements other than those discussed immediately above; *Alchornea latifolia* Swartz and *Drypetes lateriflora* (Swartz) Krug. & Urb. which occur also in the West Indies are good examples.

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The areas with the vegetation herein discussed include the eastern escarpment of the Anahuac Plateau or Central Mesa (beginning about Xilitla, San Luis Potosí, and extending through Hidalgo, Puebla, and part of Veracruz) and certain highlands in Oaxaca and Chiapas (see fig. 1). Steyermark's ('50) discussion of the flora of Guatemala suggests that the vegetation of the Cuchumatanes and the Sierra de las Minas may have much in common with that of these Mexican regions.

The eastern edge of the Central Mesa and the northeastern edge of the Mesa de San Cristóbal (fig. 1) break abruptly toward the Gulf Coastal Plain and are cut by numerous deep gorges which drain away the waters resulting from the frequent, heavy rains which characterize these areas. Where the vegetation has been removed, erosion has been extremely severe.

Climate

Much of eastern Mexico has alternating wet and dry seasons. These seasons are not always well marked, but even where they are, there are sufficient days on the escarpment with drizzles and dense fogs during the drier portion of the year to maintain the humidity above the critical point for a large number of species that would not otherwise be found there. It is noteworthy that the drier months there (November–April) generally coincide with the colder months in the United States and Canada; therefore the growing season includes essentially the same months in both areas.

The rains are usually produced by the prevailing winds from the northeast which sweep over this area dropping their moisture on the windward slopes and edges of the mesas. Due to these same winds

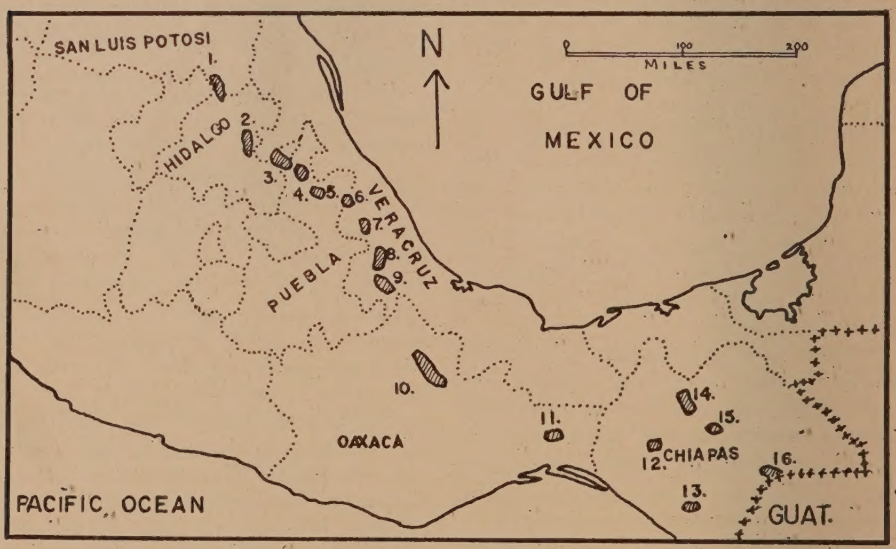

Fig. 1. Regions in Mexico where one or more of the communities described here may be found. The species *Liquidambar styraciflua* is found in all. **Key**—region of: **1.** Xilitla, S. L. P.—Chapulhuacan, Hgo.; **2.** Tianguistengo—Zacualtipan, Hgo.; **3.** Tutotepec—Tenango de Doria, Hgo.; **4.** Huauchinango—Villa Juárez, Pue.; **5.** Zacapoaxtla, Pue.; **6.** Altotonga, Ver.; **7.** Jalapa, Ver.; **8.** Huatusco—Coscomatepec, Ver.; **9.** Orizaba—Zongolica, Ver.; **10.** Cuasimulco—Choapan, Oax.; **11.** Sierra de Niltepec, Oax.; **12.** Cerro Brujo (South of Ocozocuautla), Chis.; **13.** Fincas Prusia—Liquidambar, Chis.; **14.** Pueblo—Caté (Distr. Simojovel), Chis.; **15.** Northern edge, Mesa de San Cristóbal, Chis.; **16.** Tepancuapan (Lagos de Montebello), Chis.

TABLE I. *Comparative climatic data for points in eastern temperate Mexico and southeastern United States, based on records for 24 years*

Station	Altitude in feet	Temperature °F					Precipitation in inches		
		Lowest min	Highest max	Avg for coldest month (Jan)	Avg for hottest month (May)	Avg annual	Avg annual	Avg for driest month	Avg for wettest month
Huauchinango, Puebla*	5,115	25	104	50	66	60	87.4	Feb 1.9	Sept 15.6
Jalapa, Veracruz*	4,710	36	99	58	68	64	62.0	Dec 1.8	June 11.6
Landrum, South Carolina**	1,060	−6	105	43.2	78.2†	60	60.5	Nov 3.7	July 6.6

* From data by Vivó Y Gomez, 1946.
** From data by Kincer ('41:1100).
† July.

the temperatures of the upper zone of the escarpments are relatively cool, especially during the winter season when the "northers" prevail.

Reference to table I will provide a comparison of temperature and rainfall of the eastern escarpment of the Central Mesa with the mountainous area of South Carolina. While some of the data are similar for the two areas, it must be noted that the annual variation in temperature is much smaller on the Mexican escarpment (79° F at Huauchinango, Puebla) than at the South Carolina mountain station (111° F). Also the minimum temperatures are much higher than those registered for the South Carolina station. Differences in altitude may account for the differences in temperature recorded at Huauchinango, Puebla, and Jalapa, Veracruz.

The climate of the Mexican areas mentioned is apparently the type designated as *Cfbg* in the classification of Köppen ('31).[3] For Landrum, South Carolina, Köppen's designation should be *Cfa*.

[3] In the classification of Köppen, the letters used here indicate the following climatic descriptions:

C—warm temperate rainy climates; average temperature of the coldest month below 64.4° F but above 26.6°; average temperature of warmest month over 50°.

f—no distinct dry season; less than ten times as much rain in the wettest month of summer as in the driest month of winter; less than three times as much rain in the wettest month of winter as in the driest month of summer, and the driest month of summer has more than 1.2 inches of rainfall.

a—hot summer; average temperature of the warmest month over 71.6°.

b—cool summer; average temperature of the warmest month under 71.6°.

g—hottest month comes before the summer solstice.

GENERAL GEOGRAPHICAL RELATIONS OF THE VEGETATION

Found associated in these regions with the often abundant oaks and pines are such genera as: *Alchornea, Alnus, Arbutus, Ardisia, Befaria, Beilschmiedia, Brunellia, Carpinus, Chamaedorea, Citharexylum, Conostegia, Cornus, Crataegus, Cyathaea, Drimys, Engelhardtia, Eugenia, Fagus, Gaultheria, Gilibertia, Ilex, Leucothoë, Liquidambar, Magnolia, Meliosma, Mitchella, Myrica, Nyssa, Oreopanax, Ostrya, Pedicularis, Peperomia, Podocarpus, Smilax, Styrax, Symplocos, Ternstroemia, Turpinia, Vaccinium, Xylosma,* and certain others in the Orchidaceae and Bromeliaceae.

It is not implied that all these genera are to be found throughout all of the regions under discussion nor are they all re-

stricted to them. However, here does seem to be the common meeting place for a large number of genera with varying geographical affinities.

The most conspicuous geographical element is that which seems to be related to plants in northwestern Mexico and southwestern United States. This element includes most of the pines and oaks and other genera such as *Alnus, Arbutus* and *Platanus.*

A group of genera which seems to be southern in its affinities includes: *Ardisia, Beilschmiedia, Brunellia, Buddleia, Conostegia, Cyathaea, Drimys, Ocotea, Phoebe, Podocarpus, Rapanea, Symplocos, Ternstroemia, Turpinia* and others. Perhaps as a phase of this mainly tropical element may be cited certain plants with West Indian affinities. For example, *Alchornea latifolia* Swartz and *Drypetes lateriflora* (Swartz) Krug & Urb. are common to both eastern Mexico and the West Indies. Furthermore *Beilschmiedia mexicana* (Mez) Kosterm., *Prunus samydoides* Schlecht. and *Turpinia pinnata* (Schlecht.) Hemsl. are very closely related to *B. pendula* Hemsl., *P. myrtifolia* Urb. and *Turpinia occidentalis* G. Don of the West Indies.

The floristic relationship between the highlands of Mexico and eastern United States was recognized by Fernald ('31: 52–53, 58) and was mentioned again by McVaugh ('43: 137–144). This geographical relationship has proven to be very well-marked and important in eastern Mexico. Most of the species involved have disjunct ranges with the break in northern Mexico and southern Texas. Examples include: *Adiantum capillus-veneris* L., *Asplenium monanthes* L., *A. resiliens* Kunze, *Cystopteris fragilis* (L.), Bernh., *Conopholis americana* (L. f.) Wallr., *Dichondra carolinensis* Michx., *Drosera brevifolia* Pursh, *Epifagus virginiana* (L.) Bart., *Equisetum laevigatum* A. Br., *Galium triflorum* Michx., *Gratiola virginica* L., *Houstonia angustifolia* Michx., *Hymenophyllum tunbridgense* Sm., *Hypericum mutilum* L., *Lobelia cardinalis* L., *Lycopodium alopecuroides* L., *L. cernuum* L., *L. clavatum* L., *L. complanatum* L., *Mitchella repens* L. *Osmunda cinnamomea* L., *O. regalis* L., *Pedicularis canadensis* L., *Polygala incarnata* L., *Polypodium polypodioides* (L.) Hitchc., *Sagina decumbens* (Ell.) T. & G., *Samolus floribundus* HBK., *Scirpus rubricosus* Fernald, *Specularia perfoliata* (L.) A. DC., *Spilanthes americana* (Mutis) Hier. and *Tovara virginiana* (L.) Adans. At certain places several of the above listed plants may be found associated in a single community (fig. 2).

A few of the mosses which exhibit a like type of distribution are *Aulacomnium heterostichum* Schwaegr., *Diphyscium sessile* (Schmid.) Lindb., *Pogonatum pensilvanicum* (Hedw.) Paris, *Rhodobryum roseum* (Weis.) Limpr., *Tortula caroliniana* Andrews and *T. fragilis* Wils.

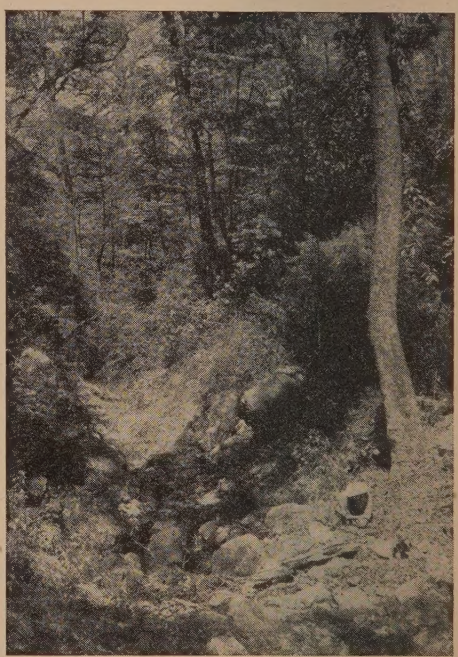

FIG. 2. Deciduous forest in a ravine at about 5,000 feet near Zacualtipan, Hgo. Among the components were: *Quercus, Pinus, Liquidambar, Tilia, Carpinus, Ostrya, Carya* and *Cercis canadensis.* Photo by A. J. Sharp, 21 Mar. 1946.

Even some of the fungi seem to have such a disjunct range. General collecting of the more easily preserved fungi from the Mexican regions (Sharp '48) resulted in a list of species over one-third of which are also found in eastern United States. Included were *Amanita caesarea* Scop., *Calostoma cinnabarina* Desv., *Fomes pinicola* Cke., *Lactarius indigo* (Schw.) Fr., *Lenzites betulina* Fr., *Pleurotus ostreatus* Fr., *Polyporus pocula* (Schw.) Berk. & Curt. and *P. cristatus* Fr.

The number of species in eastern Mexico which have very similar (probably in some cases identical) counterparts in eastern United States is large. *Fagus mexicana* Martz. is taxonomically similar to species of beech in southeastern United

TABLE II. *Known distribution in eastern Mexico and Guatemala of certain species found also in the eastern United States*

	N ←																→ S
	Galeana, Nuevo Leon	Xilitla, San Luis Potosi	Chapulhuacan, Hidalgo	Zacualtipan, Hidalgo	Tutotepec, Hidalgo	Huauchinango, Puebla	Altotonga, Veracruz, and Teziutlan, Puebla	Jalapa, Veracruz	Orizaba, Veracruz	Niltepec, Oaxaca	Sierra Madre del Sur, Chiapas	Mesa de San Cristobal, Chiapas	Cuchumatanes, Guatemala	Nebaj, El Quiche, Guatemala	Patal, Baja Verapaz, Guatemala	Sierra de las Minas, Guatemala
Acer negundo				X	X	X	X							X		
Ascyrum hypericoides				X	X	X	X	X				X		X		
Asplenium monanthes		X							X				X			
Asplenium resiliens	X	X										X				
Berchemia scandens												X			X	
Carpinus carolinianus				X	X	X	X	X	X	X	X		X	X	X	X
Cercis canadensis				X	X											
Chimaphila maculata						X						X		X		X
Chimaphila umbellata						X						X				
Conopholis americanus												X				
Cornus florida									X							
Cystopteris fragilis							X		X							
Drosera brevifolia												X				
Epifagus virginianus				X												
Equisetum laevigatum							X					X				
Fagus mexicana				X	X											
Galium triflorum								X								
Gelsemium sempervirens				X	X		X	X						X		X
Gratiola virginiana						X										
Houstonia angustifolium	X	X														
Hymenophyllum tunbridgense												X				
Hypericum mutilum						X										
Liquidambar styraciflua		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Lycopodium clavatum			X	X		X	X	X		X		X	X	X		X
Lycopodium complanatum				X	X	X	X	X	X			X	X	X		X
Lobelia cardinalis							X		X							
Menispermum canadense	X															
Mitchella repens				X	X	X	X					X				X
Nyssa sylvatica			X	X	X	X						X				
Osmunda cinnamomea						X									X	
Osmunda regalis						X						X	X		X	
Ostrya virginiana				X	X	X			X			X	X	X		X
Parthenocissus quinquefolia	X	X				X		X	X							
Pedicularis canadensis	X							X								
Pinus strobus										X			X	X		
Polygala incarnata								X								
Polypodium polypodioides		X							X							
Prunella vulgaris					X	X		X						X		
Prunus serotina	X				X	X		X						X		
Radicula nasturtium-aquatica														X		
Rhus radicans	X	X		X	X	X	X	X	X			X		X		
Rhus trilobata	X															
Samolus floribunda		X									X					
Scirpus rubricosus			X													
Smilax bona-nox						X										
Smilax glauca						X		X								
Smilax hispida						X										X
Specularia perfoliata					X	X	X									
Tovara virginiana					X	X										
Xolisma ferruginea				X	X	X	X									
Total species at each station	8	8	4	15	17	25	14	14	11	4	3	17	8	14	5	9

States; *Carya mexicana* Engelm. is similar to *C. ovata* (Mill.) K. Koch; *Leucothoë mexicana* (Hemsl.) Small, to *L. acuminata* (Ait.) G. Don; *Magnolia dealbata* Zucc., to *M. macrophylla* Michx.; *Magnolia schiedeana* Schlecht., to *M. grandiflora* L.; *Monarda malloryi* Gilly, to *M. didyma* L.; *Myrica pringlei Greenm.*, to *M. cerifera* L.; *Sambucus mexicana* Presl, to *S. canadensis* L.; and *Tilia longipes* Bush, to *T. heterophylla* Vent. Additional genera which exhibit a close relationship include: *Agrimonia, Crataegus, Desmodium, Elephantopus, Euonymus, Fraxinus, Heuchera, Ilex, Juglans, Osmorrhiza, Polygala, Pyrola, Rhamnus, Sanicula, Styrax, Vaccinium* and *Vitis*.

If the known Mexican distributions of certain identical species (table II) are examined (the data are far from complete), our attention is called to an area between Zacualtipan, Hidalgo, and Jalapa, Veracruz, and again to the Mesa de San Cristóbal in Chiapas. It seems that the greatest concentrations of the species of this element (except for the highlands of Guatemala) are in these two regions. In between and beyond these areas the number of such species diminishes.

In addition to the geographical elements mentioned above, there is a large group of endemic species in these Mexican regions. Examples include: *Chileranthemum trifidum* Oerst., *Clethra alcoceri* Greenm., *Citharexylum ligustrinum* Van Houtte, *Cleyera serrulata* Choisy, *Conostegia arborea* (Schlecht.) Schauer, *Deppea grandiflora* Schlecht., *D. microphylla* Greenm., *D. umbellata* Hemsl., *Gaultheria acuminata* Schlecht. & Cham., *Gymnanthes longipes* Muell. Arg., *Heberdenia penduliflora* (DC.) Mez, *Hoffmannia mexicana* (Link, Kl. & O.) Hemsl., *H. orizabensis* Standl., *Mahonia lanceolata* Benth., *Meliosma alba* (Schlecht.) Walp., *Microtropis schiedeana* Loesen., *Myrica pringlei* Greenm., *Ocimum sellowii* Benth., *Ocotea klotzschiana* (Nees) Hemsl., *Parathesis melanosticta* (Schlecht.) Hemsl., *Picramnia xalapensis* Planch., *Pinus patula* Schlecht. & Cham., *Platanus lindeniana* Mart. & Gal., *P. chiapensis* Standl., *Quercus acatenangensis* Trel., *Q. candolleana* Trel., *Q. excelsa* Liebm., *Q. xalapensis* H. & B., *Q. sororia* Liebm., *Q. trinitatis* Trel., *Rhamnus capraefolia* Schlecht., *Rondoletia bourgaei* Standl., *Symplocos coccinea* H. & B., *Ternstroemia sylvatica* Schlecht. & Cham., *Turpinia insignis* (HBK.) Tulne., *Viburnum microcarpum* Schlecht. & Cham. and *Zinowiewia integerrima* (Turcz.) Turcz.

Description of Some Important Forest Types

Along the upper limits of the escarpments in areas which have been little disturbed recently by man, the vegetation consists of beautiful and luxuriant forests which still occupy a rather large, but rapidly decreasing, area. It should be emphasized that these forests are being destroyed at an accelerating rate (fig. 3). Moreover, it may be that many of them are old second-growth communities which followed the inroads made on the original vegetation by the various civilizations in pre-Conquest times.

These forests contain complex communities which must be included, in a general way, in the mesophytic plant formation characteristic of temperate climates. However, it must be noted that species of many genera, e.g., *Alnus, Carpinus, Ulmus* (*Chaetoptelea*), *Cornus, Liquidambar, Nyssa, Ostrya, Platanus,* are not as clearly deciduous at these latitudes as they are farther to the north. During the years with mild winters these species retain part of their foliage until the new leaves emerge in the spring.

Moreover, a majority of the species of *Quercus* in this area have evergreen foliage, and several evergreen species of certain genera (e.g., *Befaria, Beilschmiedia, Brunellia, Buddleia, Clethra, Conostegia, Meliosma, Ocotea, Persea, Phoebe, Rapanea, Symplocos, Ternstroemia* and *Turpinia*) are very abundant.

The most important forest types, listed according to their apparent abundance,

are: Mixed oak; Pure oak; Liquidambar; Pine; Sycamore; Beech; Transition or Barranca (protected gorge); Weinmannia; and Engelhardtia. The most extensive communities in the regions discussed are included in the first five types; in contrast the last four (beech, transition, Weinmannia and Engelhardtia) are more or less limited in their distribution.

These forest types are described below in very general terms regarding their composition and habitats, followed by more detailed discussions (particularly in regard to their floristic composition) of certain communities of each at specific stations. In no case must the lists of species given be considered complete.

Mixed oak forest

The most extensive plant community is the mixed oak forest with its many variations. This most important type consists of many species of *Quercus* associated with such genera as *Carpinus, Carya, Clethra, Liquidambar, Meliosma, Nyssa, Ostrya* and *Tilia,* of which *Clethra* and *Liquidambar* are probably the most common. This forest-type is found throughout the entire escarpment area from 3,300 to 6,600 feet on steep slopes with deep soils. The mixed oak forest is characterized by variable and luxuriant vegetation in the lower layers, consisting of *Befaria, Cestrum, Conostegia, Cyathaea, Eupatorium, Oreopanax* and *Turpinia,* as well as bromeliads and orchids which occur frequently as epiphytes up to an elevation of 6,300 feet. *Liquidambar* and *Nyssa* are present in greater abundance between 3,300 and 5,000 feet than they are above that elevation. Oak forests not including these latter genera but associated with a luxuriant growth of Ericaceae (*Gaultheria, Leucothoë, Vaccinium*) grow along the upper limits of the escarpments at elevations of 6,300 to 6,600 feet near Honey, Puebla, and farther south above Yolox, Oaxaca, in the Sierra de Juárez. Along the higher stretches of the highway between Acaxo-

FIG. 3. A pure stand of young *Liquidambar* (lower center) in leafless winter condition below San Bartolo Rayón, Chis. Original forests have been destroyed here even to the mountain tops. Photo by T. MacDougall, Jan. 1950.

chitlan and Huauchinango, Puebla, there is an abundance of *Podocarpus* in the oak forest.

Analyses of the floristic composition of certain mixed oak forests follow. The lists only indicate some of the more characteristic species and are not complete. They are presented in the approximate order of their dominance.

Station A.—Near Huauchinango, Puebla, on the road to Necaxa at an elevation of about 6,550 feet is a forest on the steep northeast-facing slopes with deep soils. The average height of the forest is between 50 and 65 feet.

Trees in the overstory:

Quercus sororia Liebm.
Quercus furfuracea Liebm.
Quercus excelsa Liebm.
Clethra quercifolia Lindl.
Liquidambar styraciflua L.
Meliosma alba (Schlecht.) Walp.
Carpinus caroliniana Walt.

Small trees or large shrubs:

Cyathaea mexicana Schlecht. & Cham.
Inga sp.
Oreopanax xalapensis (HBK.) Dne. & Planch.
Oreopanax capitatum (Jacq.) Dne. & Planch.
Xylosma flexuosum (HBK.) Hemsl.
Conostegia arborea (Schlecht.) Schauer
Befaria glauca H. & B.
Turpinia insignis (HBK.) Tulne.
Turpinia pinnata (Schlecht.) Hemsl.
Chamaedorea sp.

Low shrubs:

Cestrum fasciculatum (Schlecht.) Miers
Eupatorium spp.

Epiphytes:

Diverse species of the Bromeliaceae and Orchidaceae

Station B.—There is a similar forest on 40 to 60% slopes facing the north at elevations of about 5,300 feet along the trail from Huauchinango to Pahuatlan, Puebla. The species there include *Quercus calophylla* Cham. & Schlecht., *Q. polymorpha* Schlecht. & Cham. and *Nyssa sylvatica* Marsh., among which are interspersed *Tilia longipes* Bush and *Carya mexicana* Engelm., the last shrubby and sterile.

Station C.—At an elevation of 4,620 feet between Necaxa and Tenango, Puebla, on undulating slopes with deep soil the mixed oak forest exhibits an average height of 65 feet.

Trees in the overstory:

Quercus calophylla Cham. & Schlecht.
Quercus candolleana Trel.
Liquidambar styraciflua L.
Nyssa sylvatica Marsh.
Ostrya virginiana (Mill.) Koch

Small trees or large shrubs:

Turpinia insignis (HBK.) Tulne.
Vaccinium leucanthum Schlecht.
Symplocos coccinea H. & B.
Gaultheria acuminata Schlecht. & Cham.
Palicourèa galeottiana Mart.
Rapanea ferruginea (R. & P.) Mez
Leucothoë mexicana (Hemsl.) Small
Kohleria deppeana (Schlecht. & Cham.) Fritsch

Vines:

Cissampelos pareira L.
Smilax glauca Walt.

Epiphytes:

Oreopanax capitatus (Jacq.) Dne. & Planch.
Tillandsia sp.
Epidendrum paleaceum Reib. f.

Station D.—Around Honey, Puebla, at an approximate elevation of 6,930 feet on undulating terrain and gentle slopes there is a forest the trees of which average about 50 feet in height. Some oaks there have very thick and coriaceous leaves. *Liquidambar* and *Nyssa* are absent and Ericaceous shrubs abound in the undergrowth.

Trees in the overstory:

Quercus crassifolia H. & B.
Quercus aff. *mexicana* H. & B.
Quercus stipularis H. & B.
Quercus affinis Schweidw.
Clethra alcoceri Greenm.
Clethra quercifolia Lindl.
Alnus arguta (Schlecht.) Spach
Cornus disciflora DC.
Cornus excelsa HBK.

Shrubs

Gaultheria hidalgensis Loesen.
Leucothoë mexicana (Hemsl.) Small
Citharexylum ligustrinum Van Houtte
Mahonia lanceolata Benth.
Vaccinium leucanthum Schlecht.
Vaccinium confertum HBK.
Rhammus microphylla Willd.
Chimaphila maculata (L.) Bart.

Station E.—Along the highway between Acaxochitlan and Huauchinango, Puebla, at elevations of about 6,450 feet (the higher part of the escarpment slope) *Podocarpus* is abundant among the oaks and though nearly always small (12–20 feet) and shrub-like, it readily produces flowers and seeds. At lower elevations of about 5,600 feet individuals attain heights of 50 feet.

Trees in the overstory:

Quercus trinitatis Trel.
Quercus acatenangensis Trel.
Quercus xalapensis H. & B.
Clethra quercifolia Lindl.
Ostrya virginiana (Mill.) Koch
Alnus arguta (Schlecht.) Spach
Liquidambar styraciflua L.
Crataegus pubescens (HBK.) Steud.

Small trees or high shrubs:

Podocarpus reichei Buchh. & Gray
Cornus excelsa HBK.
Vaccinium leucanthum Schlecht.
Sambucus mexicana Presl

Shrubs:

Citharexylum hidalgense Mold.
Eugenia capuli (Schlecht. & Cham.) Berg.
Deppea microphylla Greenm.
Rubus spp.
Viburnum microphyllum (Oerst.) Hemsl.
Leandra melanodesma (Naud.) Cogn.

Station F.—Surrounding the beech forest (described later) at Zacatlamaya near Zacualtipan, Hidalgo, is a mixed oak forest with the following species.

Trees:

Quercus galeotti Mart.
Quercus affinis f. *commutata* Trel.
Quercus trinitatis Trel.
Quercus xalapensis H. & B.
Liquidambar styraciflua L.
Symplocos aff. *jurgensenii* Hemsl.
Prunus samydoides Schlecht.
Phoebe sp.

Shrubs:

Heberdenia penduliflora (DC.) Mez
Gaultheria hirtiflora Benth.
Xolisma ferruginea (Walt.) Hell.

Pure oak forest

The pure oak forest is formed by one or a few species of *Quercus* with coriaceous leaves. This type occupies the drier sites such as one along the trail between the villages of Pahuatlan and Huauchinango in the northeastern part of Puebla. There at an elevation of 4,300 feet on gentle slopes is a forest of *Quercus martensiana* Trel. The trees average about 35 feet in height and are so spaced as to give the association a park-like appearance. Shrubs are very scarce but herbs are abundant during most of the year.

It was amazing to find stands of a pure oak forest composed of *Quercus oleoides* Schlecht. & Cham. occurring on flat terrain characterized by very shallow soils at an elevation of 660 feet between María Andrea and Poza Rica, Veracruz. There

they are completely surrounded by a tropical rain-forest which includes *Tabebuia pentaphylla* (L.) Hemsl., *Ficus tecolutensis* (Liebm.) Miq., *Enterolobium cyclocarpum* (Jacq.) Griseb. and species of *Gilibertia, Sapium* and *Cercropia.*

Liquidambar forest

Almost pure stands of *Liquidambar,* possibly of a secondary nature, are present on the flat or rolling lands which have deep soils near Villa Juárez and Huauchinango, Puebla, between altitudes of about 4,000 and 5,300 feet. They also occur near Huatusco-Coscomatepec, Veracruz (fig. 4), and other points farther south (fig. 3). They have a highly diverse undergrowth as indicated by the lists below.

Station A.—Near Villa Juárez at an elevation of about 4,000 feet on well-drained deep soils of gently undulating slopes is a forest 50 to 65 feet in height. The shrub layer, while not very luxuriant, is extremely varied.

Trees in the overstory:

Liquidambar styraciflua L.

Trees (20 to 35 feet in height) which are abundant:

Sambucus mexicana Presl
Beilschmiedia mexicana (Mez) Kosterm.
Prunus samydoides Schlecht.
Turpinia insignis (HBK.) Tulne.
Viburnum acutifolium Benth.

Trees (20 to 50 feet in height) less frequent:

Cyathaea mexicana Schlecht. & Cham.
Gilibertia (*Dendropanax*) *arborea* (L.) March.
Alchornea latifolia Swartz
Parathesis melanosticta (Schlecht.) Hemsl.
Symplocos coccinea H. & B.
Rhamnus capraefolia Schlecht.
Quercus sororia Liebm.
Nyssa sylvatica Marsh.
Brunellia mexicana Standl.
Buddleia americana L.
Drimys granatensis L. f. var. *mexicana* (Moc. & Sessé ex DC.) Smith
Befaria glauca H. & B.
Styrax glabrescens Benth.

Shrubs:

Drypetes lateriflora (Swartz) Krug. & Urb.
Viburnum microcarpum Schlecht. & Cham.
Bernardia interrupta (Schlecht.) Muell. Arg.
Palicourea galeottiana Mart.
Randia aculeata L.
Picramnia xalapensis Planch.
Senecio grandifolius Less.

Herbs:

Oldenlandia microtheca Schlecht. & Cham.
Senecio sanguisorbae DC.
Eupatorium sp.
Calceolaria sp.
Justicia pectoralis Jacq.
Spilanthes americana (Mutis) Hier.
Hydrocotyle mexicana Schlecht. & Cham.
Vandellia diffusa L.

Epiphytes:

Abundant bromeliads
Dichaeopsis glauca (Sw.) Schltr.

The diversity in this vegetation and the abundance of tropical elements in the above forest is probably due to its proximity to the lower altitudinal limits (about 3,500 feet) for *Liquidambar* forests where they are usually adjacent to the tropical montane rain-forest.

Station B.—On Mount Cuasimulco in the Sierra de Juárez of Oaxaca a similar *Liquidamber* (ocozotal) forest occurs at an elevation of about 4,000 feet.

Station C.—Again, much farther to the southeast of previously mentioned stations at about 4,800 feet along the margins of the lake at Montebello, Chiapas (close to the boundary of Guatemala), is a *Liquidambar* forest with pine and oak associates.

FIG. 4. Tree ferns, *Cyathaea mexicana,* in a forest of *Liquidambar* at about 4,950 feet near Coscomatepec, Ver. Photo by M. Ruiz O., 2 Nov. 1948.

On Cerro Brujo, Chiapas, *Liquidambar* has a very interesting set of associates (fig. 5). These include *Ulmus mexicana* Planch., *Alchornea latifolia* Swartz, *Phoebe helicterifolia* (Meissn.) Mez, *Rapanea ferruginea* (R. & P.) Mez, and *Eugenia* sp.

Pine forest

The pine forest, although less common than the oak forest, also covers a large area and is found more often on gentle slopes with shallow soils. Principal species which characterize this type are the mesophytic pines, *Pinus patula* and *P. pseudostrobus,* both of which have slender and flexible leaves. The undergrowth, as in most pine forests, is sparse and consists of fewer species than that of the oak forests. Stands of *Pinus strobus* L. var. *chiapensis* Martz. grow within the tropical rain-forest near Rancho de la Tomata, Tlapacoyan, Veracruz, at an altitude of about 1,800 feet. Farther south, on the slopes of Mount Cuasimulco in Oaxaca, this same type of forest grows at an approximate elevation of 3,300 feet, below the *Liquidambar* forest. A similar forest with *Liquidambar* and *Nyssa* has been located between 4,300 and 4,800 feet near Caté, district of Simojovel, Chiapas.

Station A.—Between Necaxa and Tenango, Puebla, at an altitude of about 4,600 feet there is a pine forest on shallow soils with a height which varies from 65 to 100 feet. Shrubs are present but infrequent. Vines are more frequent.

FIG. 5. Deciduous forest on Cerro Brujo at 4,950 feet about thirty miles south of Ocozocuautla, Chis. The large tree in the left foreground is *Liquidambar* and the central one is *Ulmus mexicana.* Accompanying species include: *Quercus skinneri, Alchornea latifolia, Phoebe helicterifolia, Rapanea ferruginea* and *Eugenia* sp. Photo by F. Miranda, 4 Jan. 1949.

Trees in the overstory:

Pinus patula Schlecht. & Cham.—often mixed with the following but in many places forming a pure stand.
Pinus pseudostrobus Lindl.—in many places forming a pure stand.
Quercus reticulata H. & B.—occasionally mixed in with the pines.

Shrubs:

Conostegia icosandra (Swartz) Urb.
Zinowiewia integerrima (Turcz.) Turcz.
Ascyrum hypericoides L.
Vernonia patens HBK.
Myrica pringlei Greenm.
Xolisma ferruginea (Walt.) Hell.

Vines:

Parthenocissus quinquefolia (L.) Planch.
Smilax bona-nox L.

Herbs:

Principally grasses, but also
Mitchella repens L.
Pteridium aquilinum (L.) Kuhn var. *feei* (Schaffn. ex Fée) Maxon ex Yuncker

Station B.—Near El Rancho de la Tomata, Tlapacoyan, Veracruz, at about 1,800 feet, there is a forest 65 to 100 feet in height on steep slopes with rather shallow soils.

Trees in the overstory:

Pinus strobus L. var. *chiapensis* Martínez
More or less intermixed with the pine but more often at the edge of the forest are:
Brosimum alicastrum Swartz
Cyathaea mexicana Schlecht. & Cham.
Quercus excelsa Liebm.
Brunellia mexicana Standl.
Hampea integerrima Schlecht.

Herbs:

Sauvagesia erecta L.
Spigelia sp.
Allophyton roseum (Mart. & Gal.) Pennell (*Tetranema mexicanum* Benth.)

Sycamore forest

These forests, of widths varying with the local topography, usually consist of *Platanus lindeniana* Mart. & Gal. (*P. chiapensis* Standl. in Chiapas) although they may include *Carpinus*, *Ulmus* (*Chaetoptelea*), *Liquidambar* and *Meliosma*. These sycamore forests may be found at times much below the normal limits (3,300 feet) of the community, as for example at El Paraíso (825 feet) below Villa Juárez, Puebla, and at the La Tomata waterfalls (1,650 feet) near Tlapacoyan, Veracruz. At the headwaters of the watercourses along which this type of vegetation develops, the stream beds may be invaded by dense stands of *Alnus arguta* (Schlecht.) Spach.

Station A.—On the banks of the Río Necaxa, northeast of Huauchinango, Puebla, is one example of this sycamore forest. Other species mentioned in the list are much less frequent than Platanus.

Trees in the overstory:

Platanus lindeniana Mart. & Gal.
Ulmus (*Chaetoptelea*) *mexicana* Planch.
Carpinus caroliniana Walt.
Liquidambar styraciflua L.
Nyssa sylvatica Marsh.
Gymnanthes longipes Muell. Arg.

Shrubs or herbs in moist areas along bank:

Sagina decumbens (Ell.) T. & G.
Hypericum mutilum L.
Chaptalia nutans (L.) Polak.
Senecio aschenbornianus Schauer

Epiphyte on *Platanus:*

Pitcairnia karwinskiana Schult.

Station B.—Along a brook between Coscomatepec and Huatusco, Veracruz, there is a stand (see fig. 6) differing in that some of the above species of trees are replaced with *Meliosma alba* (Schlecht.) Walp.

FIG. 6. Forest of *Platanus lindeniana* with some *Meliosma alba* along brook at about 4,900 feet between Coscomatepec and Huatusco, Ver. Photo by F. Miranda, 4 Nov. 1948.

Beech forest

These forests have been found only in two small, isolated areas within the oak forests, one at Zacatlamaya, near Zacualtipan, Hidalgo, and the other on the Cerro de Tutotepec, near Apulco, Hidalgo.[4] In both localities beech forms beautiful, almost pure forests on very steep slopes with a northern or northeastern exposure. They are restricted to an elevation between 5,900 and 6,300 feet along the upper reaches of the northeastern part of the eastern escarpment of the Mexican Central Mesa. The undergrowth includes an abundance of *Magnolia* and, less frequently, tree ferns. Bromeliads are not uncommon as epiphytes on the beech, and *Epifagus virginiana* (L.) Bart. has been found growing parasitically on beech roots at Zacatlamaya.

Station A.—The beech forest of Zacatlamaya near Zacualtipan, Hidalgo, is situated at an altitude of about 6,300 feet on very steep, north-facing slopes. The stand is dense with an average height of 100 feet. The soil is derived from a light-colored, acid, volcanic rock (perlita) which, being highly metamorphosed, is very soft and friable.

Trees in the overstory:

Fagus mexicana Martz.

Small trees and large shrubs:

Magnolia schiedeana Schlecht.
Eugenia capuli (Schlecht. & Cham.) Berg.
Turpinia pinnata (Schlecht.) Hemsl.
Sambucus mexicana Presl
Quercus trinitatis Trel.

[4] Since the completion of this manuscript, a letter from Mr. Byron E. Harrell, Minnesota Museum of Natural History, indicates that beech occurs in Tamaulipas. With his permission I quote one paragraph from his letter: "I have spent most of my time in an oak-sweet gum forest at about 3000′ above Gómez Fareis, Tamaulipas. It is a well developed forest, about 100′ high, dominated by various species of *Quercus* and by *Liquidambar*. Other important trees include *Acer, Magnolia, Podocarpus, Carya, Juglans,* and several others. A contiguous stand at about 4600′ has an abundance of *Fagus*. Most of the habitat exists on a relatively level shelf or bench between the first and second main ridges of the Sierra Madre Oriental."—A. J. S.

FIG. 7. *Fagus mexicana* at about 5,900 feet near Tutotepec, Hgo. Photo by A. J. Sharp, 27 Aug. 1945.

Shrubs:

Microtropis schiedeana Loesen.
Deppea umbellata Hemsl.
Cleyera serrulata Choisy

Epiphytes common on beech:

Tillandsia strobilifera E. Morr. ex Baker
An unidentified cactus

It is of interest that the above beech forest is surrounded by the oak woods described at station F under the mixed oak forest.

Station B.—Another beech stand with trees, the average height of which is 100 feet (figs. 7 and 8), is located at an elevation of about 5,900 feet near Tutotepec, Hidalgo. It covers the steep slopes of a V-shaped valley that drains into the deep gorge of the Río Chiflón. The soil appears to be identical with that described for the beech forest above.

Trees in the overstory:

Fagus mexicana Martz.

Small trees or large shrubs:

Magnolia schiedeana Schlecht.
Weinmannia pinnata L.
Clethra quercifolia Lindl.
Clethra alcoceri Greenm.
Quercus trinitatis Trel.
Quercus xalapensis H. & B.
Cyathaea mexicana Schlecht. & Cham.
Leucothoë mexicana (Hemsl.) Small
Ocotea klotzschiana (Nees) Hemsl.

Shrubs:

Cleyera serrulata Choisy
Viburnum caudatum Greenm.
Leandra melanodesma (Naud.) Cogn.

FIG. 8. Forest of beech (*Fagus mexicana*) with *Magnolia schiedeana* at about 5,900 feet near Tutotepec, Hgo. This area was visited three times and fog and drizzles persisted during each visit. Note tree fern (*Cyathaea mexicana*) in lower right corner. Photo by A. J. Sharp, 27 Aug. 1945.

Herbs:

Tibouchina galeottiana (Naud.) Cogn.
Coccocypselum sp.
Peperomia tenerrima Schlecht. & Cham.
Pteridium aquilinum var. *feei* (Schaffn.) Maxon

Transition or barranca (protected gorge) forest

These forests are located in the deep barrancas along the eastern escarpment between 4,000 and 5,500 feet in elevation and are characterized by the abundance of tropical elements. Many stands probably represent upward extensions of the tropical montane rain-forest which as a rule has its upper limits at elevations between 2,600 and 3,300 feet. Usually these mixtures contain a great abundance of low palms, tree ferns, members of the Lauraceae and Theaceae and shrubby Rubiaceae.

There is such a forest in a barranca on the trail from Huauchinango to Xilocuautla, Puebla, at an altitude of about 5,300 feet. The slopes of the barranca are very steep but are covered with a thick mat of slowly-decomposing organic material. In the bottom of the barranca are fragments of a forest with the following constituents.

Trees in the overstory:

Phoebe chinantecorum Schult.
Beilschmiedia mexicana (Mez) Kosterm.
Persea americana Mill. var. *angustifolia* Mir.
Turpinia pinnata (Schlecht.) Hemsl.
Cyathaea mexicana Schlecht. & Cham.

Shrubs:

Cleyera serrulata Choisy
Gymnanthes riparia Klotzsch var. *caudata* Mir.
Hoffmannia mexicana (Link, Kl. & Otto) Hemsl.

In certain places the wet soils are totally covered by the herbaceous *Peperomia mexicana* Miq.

The steeper slopes of the barranca are dominated by *Carpinus caroliniana* Walt. and *Liquidambar styraciflua* L., which may prove to represent downward extensions of the *Liquidambar* forest.

Weinmannia forest

The forests of *Weinmannia pinnata* L., frequently in almost pure stands, are limited to certain of the steeper slopes near the upper edge of the escarpment. Such communities have been seen along the trail (at about 6,600 feet) between Apulco and Tutotepec, Hidalgo, and also near Zacapoaxtla (at about 6,100 feet), Puebla, and on the slopes of Mt. Cuasimulco on the road from Yolox to Valle Nacional, Oaxaca. Fogs are very frequent in these areas, and for this reason the *Weinmannia* communities probably should be included in the fog forest type which is one of the variations of the tropical montane vegetation. At Cuasimulco, Oaxaca, the *Weinmannia* forests (fig. 9) may include species of *Quercus,* and members of the Lauraceae are often very abundant. On the higher lands near Medio Monte, between San Bartolo and Tutotepec, Hidalgo, an unusual *Weinmannia* forest includes *Magnolia* and *Leucothoë.*

Station A.—The forest near Zacapoaxtla, Puebla, is at an elevation of about 6,100 feet on moist, steep, east-facing slopes with rather shallow soils. The average height of the trees is about 25 feet.

Dominant trees:

Weinmannia pinnata L.
Turpinia pinnata (Schlecht.) Hemsl.

Other tree species:

Prunus samydoides Schlecht.
Rhamnus capraefolia Schlecht.
Quercus affinis Scheidw.
Cyathaea mexicana Schlecht. & Cham.
Oreopanax xalapensis (HBK.) Dne. & Planch.

Ternstroemia sylvatica Schlecht. & Cham.

Station B.—At an altitude of about 6,600 feet on the trail from Apulco to Tutotepec, Hidalgo, there is a pure stand of *Weinmannia pinnata* L. individuals of which vary from 25 to 35 feet in height. The forest is situated on an extremely steep, rocky slope in the upper part of the escarpment.

Station C.—The forest at Medio Monte is situated at an elevation of about 6,000 feet between San Bartolo and Tutotepec, Hidalgo. There an undulating plateau exhibits a soil formed in part from the same type of rock (perlita) as that of the beech forests described above. The arborescent forms of *Weinmannia, Magnolia* and *Leucothoë* are the largest (35 to 50 feet in height) observed in the region.

Common trees:

Weinmannia pinnata L.
Magnolia schiedeana Schlecht.
Leucothoë mexicana (Hemsl.) Small

Other tree species:

Quercus xalapensis H. & B.
Carpinus caroliniana Walt.

Engelhardtia forest

A forest of *Engelhardtia mexicana* Standl. occurs within the regions discussed here only on the Cerro de San Cristóbal near Orizaba, Veracruz. It occupies (at an altitude of about 4,600 feet) the central part of the steep, northeast-facing slopes where very deep soils occur. Above, on less steep slopes, it is replaced by a stand of gigantic specimens of *Liquidambar* (fig. 10). The mature *Engelhardtia* trees vary between 2.5 and 3.5 feet in diameter and between 100 and 135 feet in height.

Associated with *Engelhardtia* are *Ostrya virginiana* (Mill.) Koch, *Cornus florida* L. subsp. *urbiniana* (Rose) Wang., *Clethra quercifolia* Lindl. and others The smaller trees and shrubs include many species of the Rubiaceae such as *Deppea*

FIG. 9. Edge of *Weinmannia pinnata* forest at 7,000 feet protruding through the fog in the Sierra de Cuasimulco north of the City of Oaxaca. Photo by A. Castro, 27 Dec. 1940.

FIG. 10. Huge tree of *Liquidambar* in forest of *Engelhardtia* at about 4,600 feet near Orizaba, Ver. The epiphyte surrounding the trunk is *Oreopanax capitatus*. Photo by A. J. Sharp, 8 March 1946.

grandiflora Schlecht., *Rondeletia bourgaei* Standl. and *Hoffmannia orizabensis* Standl., and, in addition, *Senecio grandifolius* Less. (fig. 11).

COMMUNITIES WHICH FOLLOW FOREST DESTRUCTION

These communities are common in areas which have been disturbed by cutting timber, agriculture, or fires. The extent of such disturbances in these regions is very great and the original vegetation is fast disappearing.

Development of vegetation following single deforestation

Shrub thicket.—On steeply sloping areas in the lower part of the escarpment (from 3,300 to 4,600 feet) the clearings in the mixed oak forest and the *Luiquidambar* forest become occupied by a dense cover of high shrubs with large leaves. Common species include the powerful urticants, *Urera caracasana* (Jacq.) Griseb. and *Cnidoscolus* sp., and in addition, *Myriocarpa cordifolia* Liebm., *Bocconia frutescens* L. and *Saurauia scabrida* Hemsl., all of which are usually more frequent in the secondary growth of the tropical montane rain-forest below 3,300 feet.

These high thickets in the lower part of the oak and *Liquidambar* zones may be succeeded by a forest with *Croton draco* Schlecht., *Heliocarpus appendiculatus* Turcz. or *H. tomentosus* Turcz., *Belotia* sp. and *Trema micrantha* (L.) Blume as dominant species.

Mixed shrub and herb stands.—Areas originally covered by the mixed oak forest or the pine forest described above, which have been deforested, are invaded throughout most of the regions by pure

FIG. 11. *Senecio grandifolius* in a forest of *Engelhardtia, Liquidambar, Carpinus* and *Cornus florida* subsp. *urbiniana* at about 4,600 feet near Orizaba, Ver. Photo by F. Miranda, 1 Nov. 1948.

or mixed stands of the following shrubs and herbs:

Myrica pringlei Greenm.
Xolisma ferruginea (Walt.) Hell.
Baccharis conferta HBK.
Rubus spp.
Pteridium aquilinum var. *feei* (Schaffn.) Maxon

Meadows following repeated clearing and pasturing

Moist meadows.—If the above-described vegetation is eliminated by continual clearing and pasturing, and the soil is moist enough, meadows of grasses are formed containing species of *Panicum, Paspalum, Isachne* and other genera.

Wet meadows.—On the extremely moist soils of flat or very gently sloping terrain, wet meadows are very frequent, as for example, between Huauchinango and Xilocuautla, Puebla, where at elevations from 5,000 to 5,800 feet the vegetation consists of some or all of the following species:

Dichondra carolinensis Michx.
Spilanthes americana (Mutis) Hier.
Hypericum mutilum L.
Hydrocotyle mexicana Schlecht. & Cham.
Modiola caroliniana (L.) Don
Juncus effusus L.
Viola ciliata Schlecht.
Paspalum conjugatum Bergius
Ranunculus flagelliformis Smith
Gratiola virginiana L.
Ocimum sellowii Benth.

Not infrequently meadows of this type include *Osmunda regalis* L. and *O. cinnamomea* L., among other species.

General Ecologic and Floristic Comparisons

Even though the flora of this interesting region still needs much additional investigation, it is now possible to make some provisional observations of a general nature that will serve for the orientation of future studies.

The phanerogams of this region can be arranged according to their floristic affinities into four groups, if a few species which have a cosmopolitan distribution or other unusual relationships are omitted. The following organization is proposed:

Group I. Species of essentially tropical genera.
  Series 1. Species widely distributed in the American tropics.
  Series 2. Species endemic to Mexico or to Mexico and Guatemala.
Group II. Species of essentially north-temperate genera.
  Series 3. Species common to Mexico and the eastern part of the United States.
  Series 4. Species endemic to Mexico or to Mexico and Guatemala.

In a list of about 200 species which occur frequently in the communities previously described, 36 per cent were found to belong to series 2; 21 per cent, to series 4; 16 per cent, to series 3; 11 per cent, to series 1.

This appears to indicate that the larger number of species of the flora of eastern temperate Mexico are endemic to Mexico or to Mexico and Guatemala and are related to species distributed in tropical regions. However, it is worthy of note that the tree species belonging to the genera, *Quercus, Pinus, Liquidambar, Nyssa, Carpinus,* etc., are dominant both in regard to size of individuals and to mass of vegetation; all of these are related to species that today are amply distributed in extratropical regions to the north. They are the species which in this Mexican region determine the appearance, character and texture of the vegetation.

It appears that the larger number of species of *Quercus, Pinus, Alnus* and others, are related to other members of the same genera that grow today in northwestern Mexico and southwestern United States. In addition, there is a very interesting and characteristic phase (16 per cent of the species) of the flora of the eastern escarpment of the Anahuac Pla-

teau and similar areas toward the southeast composed of a rather large number of species common also to southeastern United States. These species, as indicated in table II, are more frequent in the region between Zacualtipan, Hidalgo, and Teziutlan, in northern Puebla, on the northern escarpment of the Mesa de San Cristóbal and on the slopes of the Cuchumatanes in Guatemala than in the intervening areas.

No other region of Mexico seems to have so many species bearing such close relationship to the vegetation of eastern United States as those described above. These areas in Mexico appear to be indicated in a general way by the known distribution of *Liquidambar* (fig. 1).

Some of these species have a disjunct rather than a continuous distribution since they are not known in the area between eastern Texas and southern San Luis Potosí or northern Hidalgo, a distance of 550 to 700 miles by land. *Liquidambar styraciflua* L., *Nyssa sylvatica* Marsh and *Mitchella repens* (fig. 12) are examples of species with this type of distribution. This gap appears to be due to the xeric nature of northern Mexico and the southern part of Texas. The report of pollen of *Abies* and *Picea* from a bog near Austin, Texas, by Potzger and Tharp ('47) suggests that in the past this region did not have the same climate as it does today and that it represented then less of a geographic barrier for mesophytic species.

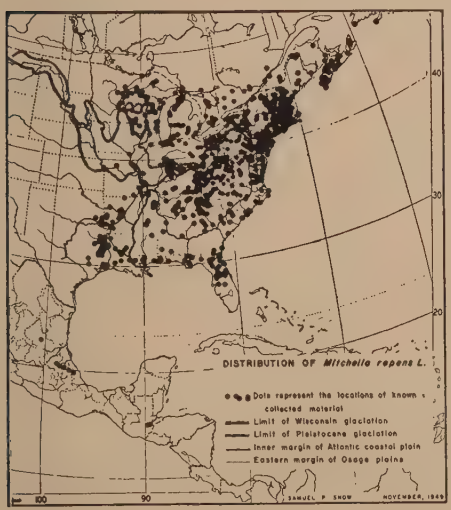
DISTRIBUTION OF *Mitchella repens* L.
Dots represent the locations of known collected material
Limit of Wisconsin glaciation
Limit of Pleistocene glaciation
Inner margin of Atlantic coastal plain
Eastern margin of Osage plains
SAMUEL P. SNOW
NOVEMBER, 1949

FIG. 12. A preliminary map of the distribution of *Mitchella repens* in North America prepared by Prof. Samuel P. Snow. The disjunction appearing in northern Mexico and southern Texas is characteristic of the distribution pattern of many species common to eastern United States and to the highlands of Mexico and Guatemala. (Map used by courtesy of McKnight & McKnight and of Prof. Snow.)

Most of the region included in this study exhibits deciduous forest of a temperate character, especially the mixed oak forest; but isolated stands of other types (fog forest, tropical montane, etc.) are also found. An understory of tropical elements is also found beneath the canopy of the deciduous forest where conditions of humidity and temperature are favorable. The mixed oak forest as a whole differs from the deciduous forest of the truly temperate (more northern) zone in two respects: 1. many of the deciduous trees are not usually completely defoliated during the winter—probably a result of mild temperatures; 2. a large number of broadleaf evergreens are an important component of this forest. The greater distribution of tropical elements is found at the lower elevations (3,300 to 4,650 feet) of the region, but it is noteworthy that the greatest concentration of *Liquidambar styraciflua* L., *Ulmus* (*Chaetoptelea*) *mexicana* Planch., *Platanus lindeniana* Mart. & Gal. and *Nyssa sylvatica* Marsh., is also at these altitudes and the frequency of these trees diminishes toward 5,600 feet. This may be due to the greater abundance of precipitation below.[5] These species are totally absent from the interior of the Mexican Plateau which has an average elevation of 6,600 feet or more.

[5] Three closely adjacent stations in Veracruz have the following elevations and averages for annual precipitation: Coatepec—4132 ft.—76.8 in.; Jalapa—4710 ft.—63.5 in.; Las Vigas—8187 ft.—54 in. Cf. Vivó and Gómez, '46.

In contrast, the fog-forest of *Weinmannia* is found on the escarpment at higher altitudes (5,600 to 6,600 feet) where fogs are more frequent.

Downward extensions of the temperate forests into the tropical montane rainforest are infrequent and consist of certain xerophytic oak stands, the sycamore forest of *Platanus lindeniana* Mart. & Gal. and isolated stands of *Pinus strobus* L. These extensions have never been observed below an elevation of 660 feet.

The strange mixture which characterizes the vegetation of this region is well illustrated by the coexistence in it of a north-temperate forest of *Quercus,* of *Fagus,* of *Liquidambar* and of *Pinus strobus* L. with tropical montane forests of *Engelhardtia,* the greatest development of which is to be found in Costa Rica, and of *Weinmannia,* best developed in Colombia where it has been studied by Cuatrecasas ('34).

Some Historical Considerations

A discussion of this flora would not be complete without reference to Berry's ('30) revision of the Eocene Wilcox flora from south-central United States. Sharp[6] found that forty-nine (30 per cent) of the 163 genera listed by Berry are known in the Mexican escarpment region described above and that forty-five others (27 per cent) are known from neighboring territory. Of these 163 genera twenty-three (15 per cent) ending in *-ites, -phyllum, -oides,* etc., could represent ancestral types of the genera now present in or near this Mexican region.

It should be noted that after allowing for errors and for the fact that this Eocene flora had a large tropical element, there is still such notable generic similarity between it and the one described above that the resemblance must not be ignored. The relationship between the Eocene Wilcox flora of the United States and the present flora of eastern Mexico will be discussed further by Sharp in a separate paper.

[6] Sharp, A. J. The relationship of the Eocene Wilcox flora to some modern floras. (Unpublished manuscript.)

Summary

The escarpment region between Xilitla, San Luis Potosí, and Orizaba, Veracruz, is described and its climate compared with that of the mountains of South Carolina. The Mexican area has equal or greater rainfall but the extremes of temperature are not so great.

The vegetation includes species closely related to those in: 1. northwestern Mexico and southwestern United States, 2. tropical regions, 3. eastern United States, 4. West Indies. In addition there is a large endemic element.

The most important plant communities are described and include: mixed oak forest, pure oak forest, *Liquidambar* forest, pine forest, sycamore forest, beech forest, barranca forest, *Weinmannia* forest, *Engelhardtia* forest; some communities which follow forest destruction are also described briefly.

Floristically the plants of the region may be divided into four categories on the basis of their geographical affinities: 1. species of essentially tropical genera, widely distributed in the American tropics; 2. species of essentially tropical genera, endemic to Mexico or to Mexico and Guatemala; 3. species of essentially north-temperate genera, common to Mexico and the eastern part of the United States; 4. species of essentially north-temperate genera, endemic to Mexico or to Mexico and Guatemala.

The present flora of eastern Mexico shares many genera with the Eocene Wilcox flora of the Mississippi Embayment described by Berry.

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HYDROIDS FROM LOUISIANA AND TEXAS, WITH REMARKS ON THE PLEISTOCENE BIOGEOGRAPHY OF THE WESTERN GULF OF MEXICO

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INTRODUCTION

Few parts of the world offer a more absolute blank to the zoogeographer of marine hydroids than the Gulf coast of Texas. Although the marine biology of the western Gulf of Mexico is probably somewhat better known than that of western Australia or Ellesmere Island, it is a fact that systematic hydroid collecting has never been done in Texas, and the recent monograph of Fraser ('44) lists only three species from that State. In the collection of the Woods Hole Oceanographic Institution, the hydroids of which are now in my hands, there are 57 samples from 20 navigation buoys in Texas waters, but most of these samples contain nothing but *Obelia dichotoma* (Linnaeus), and the list of ten species is so small that separate publication would not be justified. An additional 25 samples from Texas and Louisiana, recently received from Joel W. Hedgpeth, have proved so interesting, however, that an account of the whole material seems warranted. Permission to use the Texas records from the Woods Hole collection in advance of the full report has generously been granted by Louis W. Hutchins.

LIST OF SPECIES

The total list of 26 species is given in the following table. Of these, all except *Clytia cylindrica* L. Agassiz are new records for Texas, and the ten species (one of which is doubtfully identified) marked by asterisks are new records for the Gulf of Mexico.

**Syncoryne eximia* (Allman)
**Bimeria franciscana* Torrey
?*Bimeria humilis* Allman
Bougainvillia inaequalis Fraser
*?*Eudendrium tenue* A. Agassiz
**Hydractinia echinata* (Fleming)
**Podocoryne carnea* M. Sars
Ectopleura grandis Fraser
**Tubularia crocea* (L. Agassiz)
Clytia coronata (Clarke)
Clytia cylindrica L. Agassiz
Clytia fragilis Congdon
Clytia noliformis (McCrady)
Gonothyraea gracilis (M. Sars)
Obelia bicuspidata Clark
Obelia dichotoma (Linnaeus)
**Obelia geniculata* (Linnaeus)
**Cuspidella humilis* (Alder)
Halecium nanum Alder
Filellum serpens (Hassall)
**Sertularella gayi* (Lamouroux)
Sertularia cornicina (McCrady)
**Aglaophenia cristifrons* Nutting
Aglaophenia perpusilla Allman
Monostaechas quadridens (McCrady)
Plumularia setacea (Ellis)

NOTES ON THE SPECIES

In the following account it has seemed best not to depart from the taxonomic system of North American Atlantic coast hydroids adopted by Fraser ('44), or to repeat the synonymy given by him. Certain critical specimens from the Woods Hole collection (none of them from the Gulf of Mexico) were seen by Fraser, and there is no reason to think that my understanding of the *species* of American hydroids differs significantly from his. Fraser's views of the constitution of genera and families, however, will require considerable modification, for which this paper is not the proper place. Three species admitted to Fraser's monograph are here placed in the synonymy of other species; these are *Bimeria tunicata* Fraser, *Clytia elsae-oswaldae* Stechow, and *Obelia oxydentata* Stechow.

Syncoryne eximia (Allman)

A single fragment without gonophores from Port Aransas, though identical in all essentials with typical specimens from Washington and California, ought to be assigned to this species with considerable hesitation in view of the fact that the nearest published American record from the Atlantic side of the continent comes from Richmond Gulf. I have seen excellent material from the vicinity of Cape Canaveral, Florida, however, and less satisfactory specimens from Lake Worth Inlet and Daytona Beach, Florida, and Beaufort, North Carolina, and have no real reason to doubt that this hydroid lives in the western Gulf of Mexico. Apart from, or perhaps including these noteworthy unpublished records, the species is boreal and low-arctic in its distribution, being much commoner on the western margins of continents in the North Temperate Zone than on the eastern (see map in Hutchins, '47). There is a single record from the Southern Hemisphere at Oamaru Rocks, New Zealand (Bale, '24).

Record. Port Aransas, Tex., March 23, 1948 (Hedgpeth coll.).

Bimeria franciscana Torrey

Bimeria franciscana Torrey, '02, p. 28.
Bimeria tunicata Fraser, '43, pp. 76, 86.
Bimeria tunicata Fraser, '44, p. 50.

Fraser's *Bimeria tunicata* was founded on a single collection from the "Louisiana coast." There is little in his diagnosis to indicate how it differs from *B. franciscana* Torrey, supposedly endemic to San Francisco Bay. Comparison of the descriptions and figures in Fraser's two monographs ('37, '44) suggests that to Fraser *B. tunicata* seemed to have small, globular sporosacs arising singly from the hydranth pedicel, the stem being absolutely smooth, while the sporosacs of *B. franciscana* are ovoid and more crowded and the stem may have "a slight annulation or wrinkling in the proximal portion."

The abundant new material from Louisiana and Texas, which I have compared with the even more abundant material from San Francisco Bay in the Woods Hole collection, does not permit any such distinction to be maintained. The sporosacs are usually globular and crowded in sexually mature or old specimens but may be ovoid and are often set singly in other parts of the same colony. The perisarc of the main stem is usually thickened so greatly as to obscure the annulations that are found near the base of somewhat younger stems. Accordingly I have no hesitation in referring the Gulf of Mexico examples to Torrey's species.

The known distribution of *B. franciscana* is shown on the map (Fig. 1). The records from India, given by Leloup ('32), are extraordinary, and the distribution pattern seems at first sight to be Tethyan. As most or all of the localities are in waters of less than full marine salinity, however, it is likely that this species is a brackish-water derivative of some tropical *Bimeria,* and will be found in suitable habitats elsewhere. A statement in Fraser's book on hydroid distribution ('46, pp. 42, 109) in fact indicates that it has been found in the Potomac River.

Records. Buoys I-10, off Freeport; I-15, I-16, Houston Ship Channel in Galveston Bay; I-24, I-25, Sabine Pass (WHOI coll.).

Bay Chene Fleuri, La., May 4, 1948; no label, presumably from Corpus Christi, Tex. (Hedgpeth coll.).

"Louisiana coast" (Fraser, '43).

?*Bimeria humilis* Allman

In two of the samples from the Hedgpeth collection there is a small *Bimeria* that seems to belong to this species, but as neither group of specimens is fertile the assignment is made with some doubt. It would be reasonable to expect the species in the western Gulf of Mexico, since it occurs at Tortugas, Bermuda, the Bahamas, and Trinidad (Fraser, '44), and there are several examples in the Woods Hole collection from the east and west coasts of Florida.

Records. Palacios, Tex., May 5, 1938; Grand Isle, La., May 4, 1948 (Hedgpeth coll.).

FIG. 1. Distribution of *Bimeria franciscana* Torrey (= *B. tunicata* Fraser).

Bougainvillia inaequalis Fraser

I have considerable doubt of the validity of this species, for it seems to intergrade with *B. carolinensis* (McCrady). This statement is not based on Gulf of Mexico material, however, but on specimens from the Atlantic coast from Chesapeake Bay southward to Florida. The Texas examples agree reasonably well with Fraser's description of *inaequalis* and as they are in poor condition and infertile, and as Fraser had other specimens of *Bougainvillia* from Louisiana that he regarded as *carolinensis,* I have insufficient grounds for placing *inaequalis* into synonymy. When more collecting has been done, including medusae as well as hydroids, it may turn out that *inaequalis* is a southern or perhaps Gulf of Mexico subspecies of *carolinensis.*

Records. Buoys I-3, off Sabine Pass; I-8, I-9, off Freeport (WHOI coll.).

Off Pass a Loutre, 5 miles NNE; East Bay, La. (Fraser, '44).

?*Eudendrium tenue* A. Agassiz

This name is applied with strong reservations to a single fragment of a male *Eudendrium* with aborted hydranths above the male gonophores. The specimen is so incomplete that any designation is no more than a guess.

Record. Port Aransas, Tex., April 15, 1948 (Hedgpeth coll.).

Hydractinia echinata (Fleming)

There are two lots of this species on snail shells in the Hedgpeth collection, one identified by C. McL. Fraser. I have re-examined the specimens. The distribution of this hydroid is almost precisely the same as that of *Podocoryne carnea* M. Sars, the latter being shown on the map (Fig. 2). It is extremely common in the boreal region of Europe and North America, occurring in Labrador, Greenland, Jan Mayen, and Iceland, though unlike *P. carnea* it is not recorded from northernmost Norway or Spitzbergen. Toward the south the number of records diminishes, the only one for the Mediterranean being at Villefranche-sur-Mer, and on the American side the southernmost published record is McCrady's old one for Charleston. There is a specimen in the Woods Hole collection from the sinker of a buoy off Key West in 200 feet of water, however, so that the Texas record, though exceptionally interesting, is not the first from the Gulf of Mexico.

Records. Corpus Christi Channel, December 28, 1945, ident. C. McL. Fraser; Corpus Christi region, March, 1942, C. T. Reed (Hedgpeth coll.).

Podocoryne carnea M. Sars

Splendid and unmistakable colonies of this species occur on two empty snail shells in the Hedgpeth collection. Unfortunately the sample containing them is without a label, but correspondence with Mr. Hedgpeth indicates that it probably came from Corpus Christi Channel, December, 1945. If so, it is of great interest that the medusae were nearly ready to be liberated, for in the boreal localities where it is ordinarily collected this hydroid breeds in the summer. As shown on the map (Fig. 2), the range is strictly boreal and low-arctic, extending as far south as the north shore of the Mediterranean and into the Black Sea, while the southern limit on the American coast has previously been thought to be at Beaufort. There is a record from Saldanha Bay, South Africa (Ritchie, '07) which is not shown on the map, as it requires confirmation.

Record. No label; certainly from Texas, presumably from Corpus Christi Channel, December, 1945 (Hedgpeth coll.).

Ectopleura grandis Fraser

The large American *Ectopleura,* described from Louisiana by Fraser ('44), is not only a considerably more robust species than *E. dumortieri* (Van Beneden) but has a smaller number of tentacles when approximately mature. Fully mature specimens, with the medusae ready to be liberated, have never been seen,

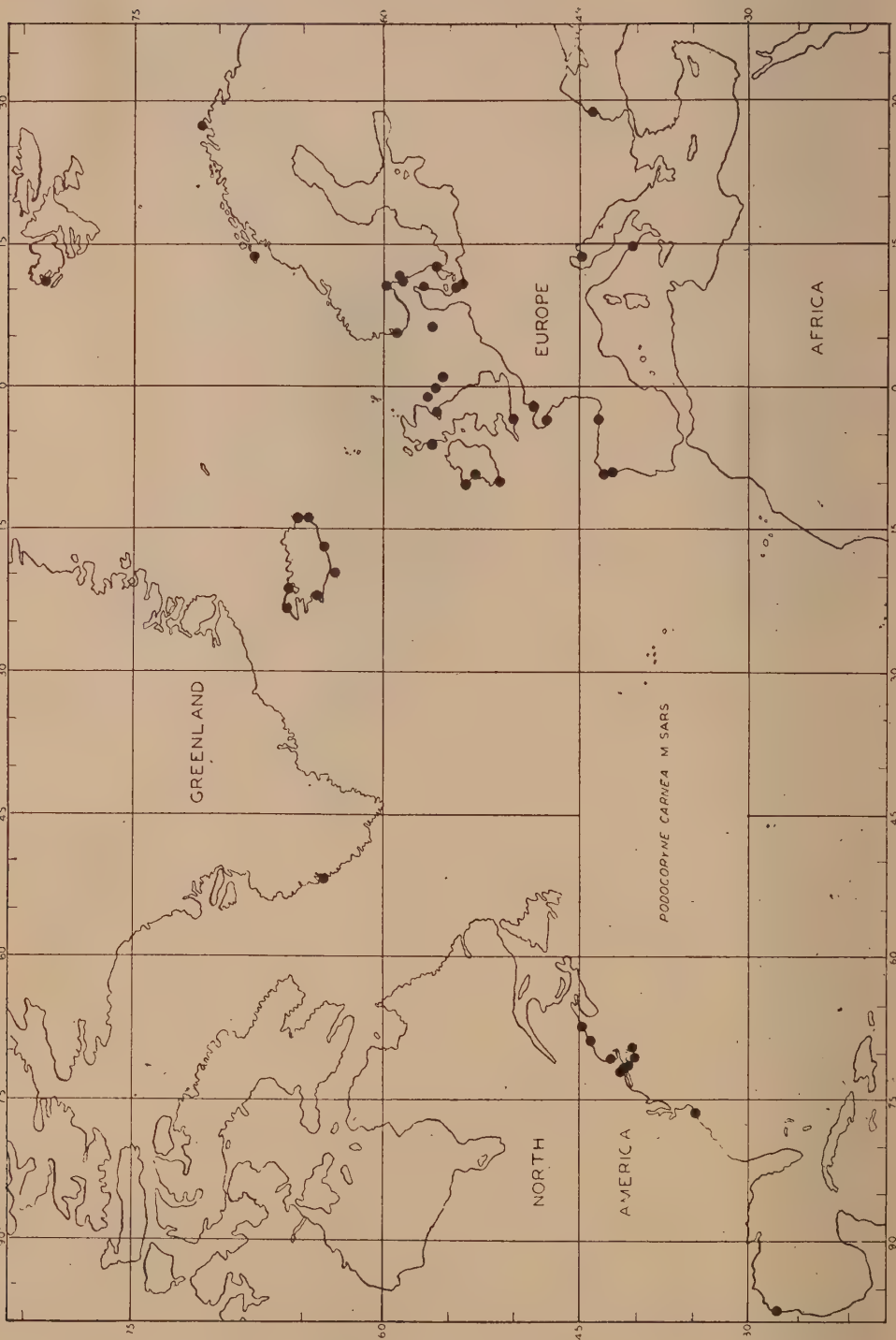

FIG. 2. Distribution of *Podocoryne carnea* M. Sars in the North Atlantic.

and, as Fraser pointed out, specimens with undeveloped medusae have probably often been confused with *Tubularia crocea* (L. Agassiz). *Ectopleura grandis,* recognizably distinct from either of the two similar species, is not endemic to Louisiana, for it is represented in the Woods Hole collection by samples from New York Harbor, Delaware Bay, off Cape Canaveral, Florida, and north of Key West, and a specimen from Long Island Sound, which has since been lost, probably belonged to this species rather than to *E. dumortieri.* The New York specimens were seen and confirmed by Fraser. The Texas examples reported here are less robust than usual, being 2 to 3 cm. high, but have 14–16 basal tentacles and 10–16 oral tentacles, as well as immature but recognizable medusae.

Records. Palacios, Tex., May 5, 1938 (Hedgpeth coll.).

Barataria Bay, Imbale Bay, and East Bay, La. (Fraser, '44).

Tubularia crocea (L. Agassiz)

When this species is mature, so that the laterally compressed apical processes can be seen on the gonophores, there is no question of its identity; otherwise it is often difficult to distinguish it from *T. larynx* Ellis and Solander, which is not always so completely annulated a species as the descriptions indicate. Of the three Texas collections examined, all of them from Port Aransas, two are unquestionably *T. crocea,* while the third is more doubtful owing to immaturity.

The distribution of this familiar hydroid conforms to the "American" pattern, which is not uncommon among hydroids though infrequent among other marine organisms. The records regarded as valid and not based on introduction by shipping have been entered on the map (Fig. 3). The Texas records may not be the first from the western Gulf of Mexico, for Fraser ('46, p. 144) referred to "somewhat doubtful reports from Palm beach, Fla., and the Louisiana coast." From a preliminary examination of the Woods Hole collection I have no doubt that it occurs at least as far south as Daytona Beach, Florida, but it seems to be entirely lacking from the tropical Atlantic, and the records from the tropical Pacific (Fraser, '38) therefore seem somewhat questionable, though there are no other grounds for rejecting them. Reports from the Southern Hemisphere by workers not thoroughly familiar with the species, however, have not been included on the map. According to Broch ('14) it occurs at Luderitz Bay, South Africa, and Hartlaub ('05) reported it from Valparaiso, Chile. I have not located in the literature the record from the Straits of Magellan referred to by Fraser ('46, p. 144), though there is an obviously invalid record from the hull of the "Gauss" in the South Atlantic (Vanhöffen, '10). The species has been introduced on shipping at Plymouth, England, and is apparently well established there (Marine Biological Association, '31), but is not known to have spread elsewhere in European waters.

Records. North jetty, Port Aransas, Tex., March 20, 1947 (immature); buoy, Port Aransas, Tex., April 14, 1948; Port Aransas, Tex., December 15, 1947 (Hedgpeth coll.).

Clytia coronata (Clarke)

This is a familiar member of the tropical flotsam fauna, and its occurrence in Texas waters is not unexpected, especially as it has previously been reported from Louisiana. Though common in the American tropics on both sides of the Isthmus of Panama, and borne as far north as Nantucket Shoal, it has apparently not been found in the western Pacific or the eastern Atlantic.

Records. Buoy I-3, off Sabine Pass (WHOI coll.).

On driftwood, Port Aransas, Tex., April 13, 1948; on *Sargassum,* Port Aransas, April 26, 1948; on *Sargassum* and tar, Port Aransas, April 16, 1948; Port Aransas, December 15, 1947; Palacios, Tex., May 5, 1938; Grand Isle, La., May 4, 1948 (Hedgpeth coll.).

Grand islet and Pass Christian, La., on floating seaweed (Fraser, '44).

FIG. 3. Distribution of *Tubularia crocea* (L. Agassiz). The northern limit is believed to be fixed approximately by the isothere 55° F (= 12.8° C). On the Atlantic and Gulf coasts, but not on the Pacific coast, the southern limit coincides with the isocryme 70° F (= 21.1° C). See discussion in text.

Clytia cylindrica L. Agassiz

Clytia (*Platypyxis*) *cylindrica* L. Agassiz, '62, p. 306
Thaumantias (*?*) *elsae-oswaldae* Stechow, '14, p. 122
Clytia elsae-oswaldae Stechow, '14, p. 125
Clytia cylindrica Fraser, '44, p. 134
Clytia elsae-oswaldae Fraser, '44, p. 136

In erecting his *Clytia elsae-oswaldae,* Stechow said:

"Diese form steht *Clytia cylindrica* (L. Ag.) nahe, unterscheidet sich aber von ihr besonders durch ihre viel gröbere Form, ihre viel längeren Thekenstiele, ihre relativ nicht so tiefen Theken, und ihre stets nur an der Hydrorhiza entspringenden Gonotheken."

None of these characters seems to be of specific value, with the possible exception of the last (gonophores on the stolon, not on the stem), and I have seen specimens in which the gonophores are borne *both* on the stem and on the stolon. The character used by Fraser to separate the two species from Stechow's description is one mentioned more casually by Stechow, namely that the margin of the hydrotheca is sinuous in outline, but this feature is ordinarily shown by typical *C. cylindrica.* Stechow's species therefore falls into synonymy, and the Gulf of Mexico specimens are referred to the widespread *C. cylindrica.*

Though it is common everywhere on the Atlantic coast of the United States and in the Caribbean, and is more or less continuously distributed from the Queen Charlotte Islands to Peru, this species has been reported outside American waters only from Japan (Fraser, '46, p. 214), and I have not located the latter record. It is the only species of the present report previously recorded from Texas (Fraser, '44).

Records. On *Sargassum,* Port Aransas, Tex., April 26, 1948; on *Sargassum* and tar, Port Aransas, April 16, 1948; Palacios, Tex., May 5, 1938; from female blue crab, Station 17 (Texas Game, Fish, and Oyster Commission); Grand Isle, La., May 4, 1948 (Hedgpeth coll.).

East Bay, La.; Gulf coast of Texas (Fraser, '44).

Clytia fragilis Congdon

This species differs very little from *C. cylindrica* except in its more prolific branching and in the shape of the hydrotheca, which is deeply campanulate rather than cylindrical. The specimens in the Hedgpeth collection are in poor condition, so that the margin of the hydrotheca cannot be made out, and they would not be given a specific name were there not excellent (though sterile) material from Texas in the Woods Hole collection. The species seems to be restricted to the region from the Bermudas to Puerto Rico; the only previous record from the Gulf of Mexico is from the Tortugas, and is given by Leloup ('37) under the name *Laomedea tottoni* (see Fraser, '44).

Records. Buoy I-25, Sabine Pass (WHOI coll.).

Port Aransas, Tex., December 15, 1947 (Hedgpeth coll.).

Clytia noliformis (McCrady)

This is another common member of the *Sargassum* fauna, previously reported from Louisiana, and its occurrence in Texas waters is not surprising. A number of records come from fairly high latitudes, as far north as Nova Scotia, for example, but Fraser ('46) believed, no doubt correctly, that these are *Sargassum*-borne. The species has not been taken in the tropical eastern Pacific, but otherwise might be called pan-tropical.

Records. On *Sargassum,* St. Joseph Island, Tex., April 10, 1946 (Hedgpeth coll.).

Grand Isle, La. (Fraser, '44).

Gonothyraea gracilis (M. Sars)

This is a widespread but rather uncommon species, represented in a single sample from Texas in the Woods Hole collection, but previously reported from Louisiana. The distribution, shown on the map (Fig. 4), is of unusual interest. The species occurs almost everywhere in the Northern Hemisphere from Iceland and Alaska to the Equator, but penetrates the Southern Hemisphere only along the

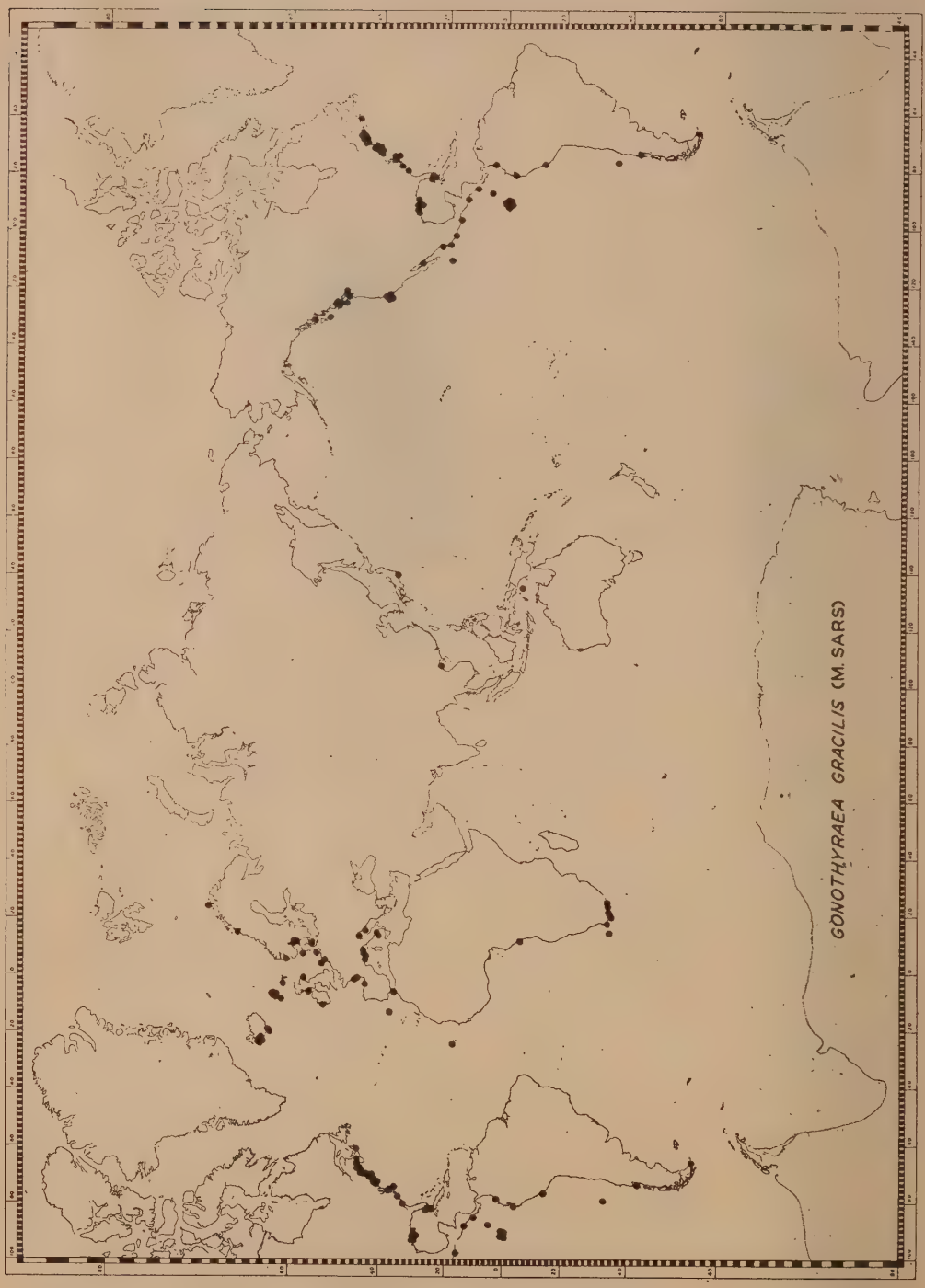

FIG. 4. Distribution of *Gonothyraea gracilis* (M. Sars).

western sides of continents, being unknown from Australia and New Zealand and in the Indian Ocean. The northern limit appears to be in the Murman Sea, which is not an arctic locality; according to Fraser ('46, p. 210) it also occurs in Greenland, and this is barely possible, but I have found no Greenland records.

Records. Buoy I-24, Sabine Pass (WHOI coll.).

From mangrove swamps at Bayou Pass, Grand Isle, and East Bay, La. (Fraser, '44).

Obelia bicuspidata Clark

Obelia bicuspidata Clark, '76, p. 58
Obelia oxydentata Stechow, '14, p. 131
Laomedea spinulosa var. *minor* Leloup, '35, p. 26; Leloup, '37, p. 98
Obelia bicuspidata Fraser, '44, p. 153
Obelia (?) oxydentata Fraser, '44, p. 164

This is a variable species, and is probably known under many names. More precisely, it has not often been taken when sexually mature, and the immature forms have received several different names. The form known as *O. oxydentata* Stechow is common in the American tropics; I have seen it in samples from the east and west coasts of Florida, the Bahamas, and Panama. It appears to me to be identical with *O. bicuspidata* in all respects except the lack of a fascicled stem, and as it never bears gonophores I have no doubt that it is merely a juvenile.

O. bicuspidata is a pan-tropical species, extending into temperate waters in both directions from the tropics. In the Northern Hemisphere it occurs as far north as Casco Bay (Maine), the Zuider Zee, Sagami Bay (Japan), and San Francisco Bay; in the Southern Hemisphere it extends to Brazil and to Port Jackson, Australia, but there are no records from the eastern sides of the South Atlantic and South Pacific, and in the Indian Ocean it is so far known only from the Indian peninsula. *O. spinulosa* Bale may be a distinct species, for it appears to differ in the gonosome, but if so it is confined to the western Pacific and the Indian Ocean. The American records for *O. spinulosa* var. *minor* (Leloup) certainly should be referred to *O. bicuspidata.*

Records. Buoy I-24, Sabine Pass (WHOI coll.).

Port Aransas, Tex., October 31, 1947; Port Aransas, November 20, 1947; Grand Isle, La., May 4, 1948 (the latter specimens fertile, with fascicled stems) (Hedgpeth coll.).

Shore and on *Sargassum,* Grand Isle; in mangrove swamp, Bayou de Gettes; Hog Island, Barataria Bay (Fraser, '44).

Obelia dichotoma (Linnaeus)

This is one of the commonest shallow-water hydroids of the Northern Hemisphere, and it is surprising that it has not been previously reported from the western Gulf of Mexico, though it is known from the Tortugas. It is the only species represented in the majority of samples in the Woods Hole fouling collection. As shown on the map (Fig. 5), the range is extensive, though by no means cosmopolitan: not only does it stop approximately at the Equator, but the species is absent from the Indian Ocean.[1] Furthermore, though there are records from the Arctic and from deep in the tropics, by far the greatest concentration is in the boreal region, and this cannot be entirely a result of unequal collecting effort.

Records. Buoys I-3, I-4, off Sabine Pass; I-5, Galveston Bay; I-7, Sabine Bank; I-9, I-10, off Freeport; I-13, I-14, off Matagorda Island; I-19, I-20, Sabine Pass; I-21, off Freeport; I-22, I-23, I-24, Sabine Pass (WHOI coll.).

On driftwood, Port Aransas, Tex., April 13, 1948; south jetty, Port Aransas, October 20, 1947; on oysters, Port Aransas, October 31, 1947; from female blue crab, Station 17 (Texas Game, Fish, and Oyster Commission); on *Sargassum* and tar, Port Aransas, April 16, 1948; Port Aransas, November 20, 1947 (Hedgpeth coll.).

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[1] There is a problematical record from "St. Paul, Novara Expedition" (Marktanner-Turneretscher, '90). The "Novara" visited St. Paul Island (Lat. 38° 42′ S., Long. 77° 34′ E.) in the southern Indian Ocean, but not St. Paul Rocks on the Mid-Atlantic Ridge. There is no doubt from Marktanner's description that the species has been identified correctly, but the accuracy of the label is open to suspicion. Certainly any record from the Southern Hemisphere requires confirmation.

FIG. 5. Distribution of *Obelia dichotoma* (Linnaeus)

Obelia geniculata (Linnaeus)

Like the preceding species, this hydroid is widespread, extremely common in the boreal region, and has not been reported previously from the western Gulf of Mexico. It is the closest approach to a truly cosmopolitan species known among hydroids. The only extensive body of water from which it is absent is the northern Indian Ocean, and this is doubtless a reflection of its general uncommonness in warm waters, for it occurs at St. Paul and Macquarie Islands in the southern Indian Ocean, and is probably continuously distributed in the whole antiboreal region as it is in the Northern Hemisphere. It penetrates into the Arctic as far as Spitzbergen and Jan Mayen, and into the Antarctic to Auckland and Campbell Islands and South Georgia. It is not known from the tropical western Atlantic or at the Tortugas, but among the rare tropical records are those from the Galapagos and Amboina.

Record. Buoy I-19, Sabine Pass (WHOI coll.).

Cuspidella humilis (Alder)

This exceedingly minute species is probably the most easily overlooked of all hydroids. It is rather similar to *Lafoeina tenuis* M. Sars, and can be confused with it if the nematophores characteristic of the latter species are not specifically searched for. In the Arctic and northern European waters both species have been reported by reliable observers; a few specimens of *L. tenuis* from warmer regions may have been carelessly referred to *C. humilis* on geographic grounds, though it is not very probable. At any rate the geographic grounds do not exist, for *L. tenuis* has recently been taken off Morocco (Kramp, '46) and is abundant in the Woods Hole collection as far south as southern Florida and the Bahamas. So far as the records show *C. humilis* is predominantly a boreal and low-arctic species, occurring from East and West Greenland and the Arctic coast of Siberia to the Mediterranean and from the Queen Charlotte Islands to San Francisco Bay. There are several records from the tropics, however, namely from the Cape Verde Islands, Lower California, and Colombia. The distribution pattern recalls that of *Obelia dichotoma* in that an ordinarily boreal species extends to the Equator in places. It has been previously recorded from the Atlantic coast of North America only from Georges Bank and Beaufort.

Record. Buoy I-8, off Freeport (WHOI coll.).

Halecium nanum Alder

This is a minute, creeping species, ordinarily found on *Sargassum*, but occurring on buoys in southern Florida. I have not seen the gonosome. The hydroid is so small as to be easily overlooked, and this probably accounts for the paucity of records, for those that are known to me are widely scattered. It is not uncommon in the Caribbean region, and there are three records from the tropical eastern Pacific from Lower California to Panama, but outside American waters it is known only from France, Japan, and western Australia, and doubtfully from Naples. Fraser ('46, p. 261) implies that it occurs in the Azores, as it quite probably does, but I have not found this record in the literature. The species is doubtless pan-tropical, but, being *Sargassum*-borne, it has been reported as far north as Nantucket and will presumably turn up in Iceland. The new record from Texas is on *Sargassum*.

Record. On *Sargassum* and tar, Port Aransas, Tex., April 16, 1948 (Hedgpeth coll.).

Filellum serpens (Hassall)

Another "cosmopolitan," *F. serpens* would be expected to occur in the western Gulf of Mexico, or almost anywhere else except the Indian Ocean. Though the number of records is smaller, the range is essentially that of *Obelia geniculata:* from the Arctic to the Antarctic, commonest in the boreal and antiboreal regions, and

rare in the tropics. The arctic records are somewhat more numerous than those of *Obelia*, and the tropical records are numerous only in the eastern Pacific, though it has been reported from the Tortugas, at various places in the Caribbean, and at the Cape Verde Islands. In the Antarctic the range extends beyond that of *Obelia* to the Antarctic continent itself, but appears to be confined to the American quadrant.

Records. Buoys I-8, off Freeport; I-15, I-16, Houston Ship Channel in Galveston Bay; I-25, Sabine Pass (WHOI coll.).

Sertularella gayi (Lamouroux)

A single fragment, branched but not showing enough of the stem to determine its nature, agrees in all available characters with this species. The identification requires confirmation from better material, but *S. gayi* would be expected in the western Gulf, for it is well known in the nearby waters of the southern United States and the Caribbean. Outside American waters, where it occurs as far north as the Gulf of St. Lawrence, its distribution is puzzling, probably because it lives in relatively deep water and is inadequately collected. Its center of distribution seems to be the North Atlantic, for it is common in Europe from Iceland to Madeira, and is reported from stations as far south as the Cape of Good Hope, Gough Island, and Patagonia. The species appears to be totally absent from the eastern Pacific, but there are scattered records from Japan, the East Indies, Australia, and the western Indian Ocean.

Record. Port Isabel Channel, Tex., March 15, 1947 (Hedgpeth coll.).

Sertularia cornicina (McCrady)

The taxonomy of the division of *Sertularia* to which this species belongs is in a thoroughly confused state. I have no doubt that the specimens reported here belong to McCrady's species as recognized by Fraser, and they agree with Billard's ('25) description and figures of the "Siboga" specimens. But Billard's list of synonyms is perhaps too inclusive, and a great deal of material will have to be examined to decide the limits of *S. cornicina*. Taking Billard's conception at its face value, the species is pan-tropical, reaching latitudes nearly as high as those attained by *Plumularia setacea* (Ellis) (see map, Fig. 6). It is common in the Caribbean and elsewhere in the western tropical Atlantic as well as in the Mediterranean, and appears under one or another name in the western Indian Ocean, Ceylon, the Andaman Islands, throughout the East Indies, at Easter Island, and in the eastern Pacific from California to the Galapagos. The poleward limits are probably not very meaningful, since the species is *Sargassum*-borne, but it has been reported from Nova Scotia, Sagami Bay (Japan), Santos (Brazil), and the Sir Joseph Banks archipelago south of Australia.

Records. Port Isabel, Tex., May 15, 1946; on *Sargassum*, Port Aransas, April 26, 1948 (Hedgpeth coll.).

Aglaophenia cristifrons Nutting

This is a very inadequately known species, like many others of its family. I have not seen the gonosome, but the trophosome of the Texas specimens agrees so exactly with the descriptions and figures of Fraser and Nutting that there seems to be no doubt of the identification. The deep-water *Aglaophenias* have been collected so seldom that a new record from Texas for a species previously known only from off Havana should occasion no surprise.

Record. Epizoic on *Podochela sidneyi*, Port Isabel, Tex., May 1, 1947 (Hedgpeth coll.).

Aglaophenia perpusilla Allman

This is a minute, *Sargassum*-borne species, closely similar to *A. late-carinata* Allman and having the same general range, but considerably less common in collections. Unlike the latter species it is not yet known outside the American tropics (and the American temperate localities to which *Sargassum* is commonly

carried). All of the specimens examined were collected in April, the month when *Sargassum* is found on the Texas coast in greatest quantities, and were sterile. It is possible that there is a seasonal cycle of dominance by *Aglaophenia* species in the *Sargassum* community, or it may be that these Texas gulf-weeds belonged to an unusual type, so that a substratum preference is involved (see Parr, '39); *A. late-carinata* is the only species previously reported from Texas, though the very different *A. rigida* Allman has been taken in Louisiana. Certainly two species so closely related as *A. perpusilla* and *A. late-carinata* are not likely to occur on the same piece of *Sargassum*.

Records. On *Sargassum,* St. Joseph Island, Tex., April 16, 1946; on *Sargassum,* Port Aransas, April 26, 1948; on *Sargassum* and tar, Port Aransas, April 16, 1948 (Hedgpeth coll.).

Monostaechas quadridens (McCrady)

This is a familiar species in tropical American waters, and while it has not often been collected elsewhere, perhaps because it so often lives in fairly deep water, it appears to be genuinely pan-tropical.

Record. Epizoic on *Podochela sidneyi,* Port Isabel, Tex., May 1, 1947 (Hedgpeth coll.).

Plumularia setacea (Ellis)

This is a common species in the warmer waters of the world, and is almost as well known in some parts of the boreal region. As the map (Fig. 6) shows, it is a pan-tropical hydroid with a tolerance for low temperatures unusual in tropical animals. Its penetration into temperate latitudes, however, is not uniform, but is noticeably greater along the eastern sides of oceans than on western, presumably because it requires relatively high winter temperatures for survival. Thus it lives in the eastern Pacific from Kodiak Island to Chile, and in the eastern Atlantic from Iceland to South Africa, but in the western Atlantic it has not been taken north of Marthas Vineyard or south of Santos, Brazil. Unfortunately the poleward limits of dispersal are probably not reliably obtained from the published records, for the species often lives on *Sargassum* and other flotsam.

Records. On *Sargassum,* St. Joseph Island, Tex., April 16, 1946; on *Sargassum* and tar, Port Aransas, April 16, 1948 (Hedgpeth coll.).

Other Species Reported from Louisiana and Texas

In order to complete the account of hydroids known so far to occur in the western Gulf of Mexico, the following lists of species have been compiled from Fraser's monograph ('44).

Six species of "American" distribution have been reported from Louisiana or Texas:

Obelia equilateralis Fraser (Ecuador, Louisiana)
Obelia obtusidens (Jäderholm) (Chile, Ecuador, Louisiana)
Sertularia inflata (Versluys) (Galapagos, Woods Hole to Trinidad, eastern tropical Atlantic)
Aglaophenia rigida Allman (eastern tropical Pacific, Atlantic coast of U. S., Azores)
Plumularia floridana Nutting (eastern tropical Pacific, Atlantic coast of U. S.)
Schizotricha tenella (Verrill) (eastern tropical Pacific, Atlantic coast of U. S.)

Four Louisiana species are almost certainly pan-tropical, though one of them (*Aglaophenia late-carinata* Allman) is known outside the Atlantic only from Madagascar:

Clytia longicyatha (Allman)
Pasya quadridentata (Ellis and Solander)
Aglaophenia late-carinata Allman
Plumularia diaphana (Heller)

There are two American boreal Atlantic species that presumably reach their southern limits in Louisiana:

Bougainvillia carolinensis (McCrady)
Bougainvillia rugosa Clarke

FIG. 6. Distribution of *Plumularia setacea* (Ellis).

Finally, there is one species, *Cordylophora lacustris* Allman, that lives in brackish or fresh water, and is likely to occur in estuaries almost anywhere. It is known from most regions of the world, including the interiors of the American and Eurasiatic continents, but is usually found isolated in ports; doubtless it is commonly distributed as a fouling organism on ships. It happens to have been collected in Louisiana, and may well live in the Houston Ship Channel in Galveston Bay, though it did not appear on the two buoys examined from that locality.

Note added in proof: According to Mr. Hedgpeth, who sent some hydroids to Fraser, *Zanclea costata* Gegenbaur should be added to the list of (presumably pantropical) species previously reported from Texas. This identification is given in a letter from Fraser to Hedgpeth dated October 18, 1946. The material was collected March 3, 1946, in a "fist-sized clump cast on beach, Port Aransas," and included *Ectopleura grandis* and *Gonothyraea gracilis* in addition to *Zanclea.* An identification of *Bougainvillia inaequalis,* from piling, Aransas Bay, March 14, 1946, is given in the same letter. The addition of one more problematical *Sargassum*-borne species, bringing the total list for the western Gulf of Mexico to 40, in no way affects the zoogeographic argument given below.

Zoogeographic Discussion

Twenty-five new hydroid records from Texas waters are reported here, but it would be absurd to pretend that the hydroid "fauna" of the western Gulf of Mexico is now well known. Only 21 species were previously recorded from casual collecting in the region, three of them (*Clytia cylindrica, Sertularia inflata,* and *Aglaophenia late-carinata*) from Texas and 20 from Louisiana. The total of 39 species now listed is certainly low, and the impression of impoverishment may turn out to be correct. But future collecting will surely bring other species to light, and a statistical comparison with the Florida Keys, where about a hundred species have been collected, would be premature.

Furthermore, the application of statistical methods to biogeography is fallacious, if it requires the synthesis of ranges of individual species, each of which is governed by laws differing from those of every other species. Customarily such a synthesis results in a "fauna," which is then "analyzed" to discover its "affinities" with other faunas. It has never been made clear how an analysis of an artificial assemblage, arrived at by putting disparate elements together, can yield more useful results than a study of the elements themselves. The terms "arctic," "temperate," "boreal," and "tropical" have been loosely used in the preceding pages; they will continue to be useful provided no attempt is made to make them precise. Efforts to define "provinces" and "sub-provinces," or to draw boundaries between the "warm-temperate" and the "cold-temperate" or "sub-tropical" faunas, such as are made by Ekman ('35) among many others, are doomed to failure.

Objections to the traditional methodology of biogeographers have been stated at some length in a review, "Biogeography of the Pleistocene" (Deevey, '49), and need not be stressed here. Our immediate concern is to explain the occurrence in the western Gulf of Mexico of a number of hydroids of distinctly boreal distribution. These hydroids are discontinuously distributed from the Atlantic coast of the United States to Louisiana and Texas, for *apparently they do not live* in southern Florida or in the Tortugas. In one case enough is known about the species to say that in all probability *it could not live* in southern Florida. The problem would exist (though it might be more easily ignored) if only one species, such as *Tubularia crocea* or *Podocoryne carnea,* displayed this distribution pattern, and no generalization or synthesis is implied by the statement that a number of species do

so. But one such example of disjunct range might be the result of an accident, either of dispersal or of collecting, and the repetition of the phenomenon merely increases the likelihood that the problem is real.

The discussion will take the form of an attempt to decide whether a schema (such as that of Hutchins, '47) that regards biogeography as the by-product of existing distributions of ecological factors, temperature in particular, can explain this curious distribution, or whether historical factors have also to be called into account.

Zonal typology

In a work of fundamental importance to marine biogeography Hutchins ('47) has recently proposed a codification of ranges of species along the coastlines of the world, resting his system on the assumption that temperature is the most important single factor controlling such ranges. It is unfortunate, though inevitable, that the work is largely deductive, and few specific examples are given. Hutchins pointed out that the use of the mean annual temperature for the construction of boundaries of ranges is highly misleading, and that isotherms measuring the lowest and highest temperatures ordinarily experienced by an organism during the course of its life are much more useful to the biogeographer. Such isotherms can be plotted rather accurately over land, and have often been used by workers in terrestrial ecology in much the way suggested by Hutchins. For the sea surface the requisite data are just beginning to be assembled, and as a first approximation to the biologically significant temperature boundaries Hutchins used generalized, small-scale charts showing the mean temperature of the coldest and warmest months. Isotherms connecting points approximately equivalent for these two variables are called isocrymes and isotheres, respectively, and the methods by which the charts have been constructed were discussed by Hutchins and Scharff ('47) and by Fuglister ('47); the latter author gave a more detailed picture for the western North Atlantic, including the Gulf of Mexico.

A priori, it is clear that four different kinds of reaction to temperature on the part of an organism will determine four biogeographic types. Type 1 species are those whose equatorward limits are set by the occurrence of summer temperatures too high for survival (an isothere), and whose poleward limits are related to winter temperatures too low for survival (an isocryme). Type 2 species have their boundaries fixed by the critical temperatures required for spawning or some other phase of the reproductive process, the equatorward limit being set by an isocryme representing temperatures too high for breeding and the poleward limit corresponding to an isothere beyond which temperatures never reach the critical level. For Type 3 the summer temperatures (isotheres) are limiting in both directions, but the equatorward limit is fixed by temperatures too high for the survival of the adults, while the poleward limit is bounded by water too cold for breeding. In Type 4, the converse of Type 3, both limits correspond to isocrymes, the equatorward dispersal being prevented by temperatures too high for reproduction and the poleward dispersal by temperatures so low that the adults cannot survive.

When temperature ranges on several coastlines are compared in the light of this scheme, it becomes obvious that species having identical ranges on one coast can belong to four different types, each of which will have a different range on some other coast. This shows at once that the attempt to define a "boreal" or a "subarctic" province after the fashion usual in biogeography is based on a misconception. The immense merit of Hutchins' proposal consists in this, for it is literally "Biogeographie vom Tier aus" (Broch, '25). Difficulties appear, however, when we begin to apply it to real cases. In most instances we have no way of deciding what temperatures are actually limit-

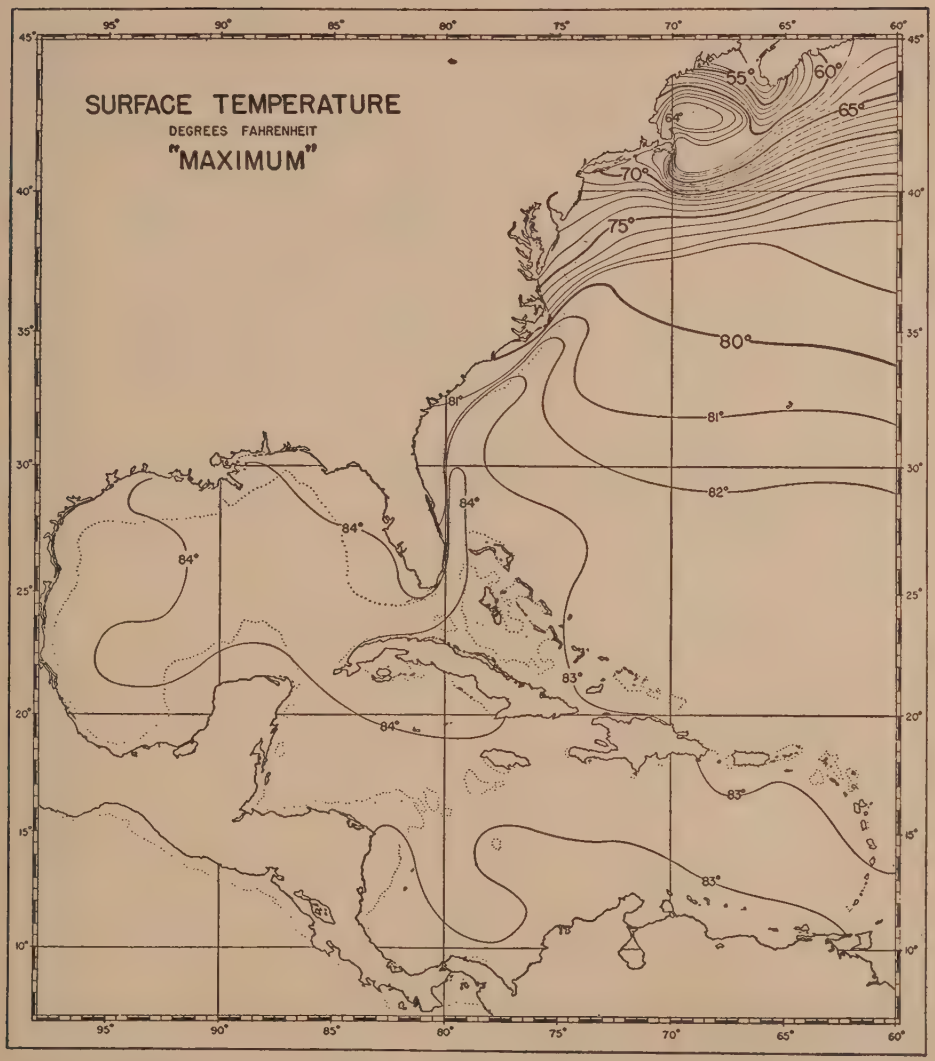

FIG. 7. Sea-surface isotherms for the mean Fahrenheit temperature of the warmest month (*isotheres*) in the western Atlantic. From Fuglister ('47), Plate 13.

ing the ranges of species except to compare their limits on two or more coasts. This is a hazardous procedure, likely to lead to circular arguments, and fails completely where endemic species are involved. The cases of *Balanus balanoides* and *Mytilus edulis,* given by Hutchins as examples of Types 2 and 3, respectively, are probably valid because there is evidence of other sorts (laboratory experiments, observations of critical temperatures for spawning and for attachment to test panels as fouling organisms) from which some idea of the limiting temperatures can be obtained. On the other hand, the example of *Syncoryne eximia,* tentatively offered as Type 1 purely on the basis of its range as known when Hutchins

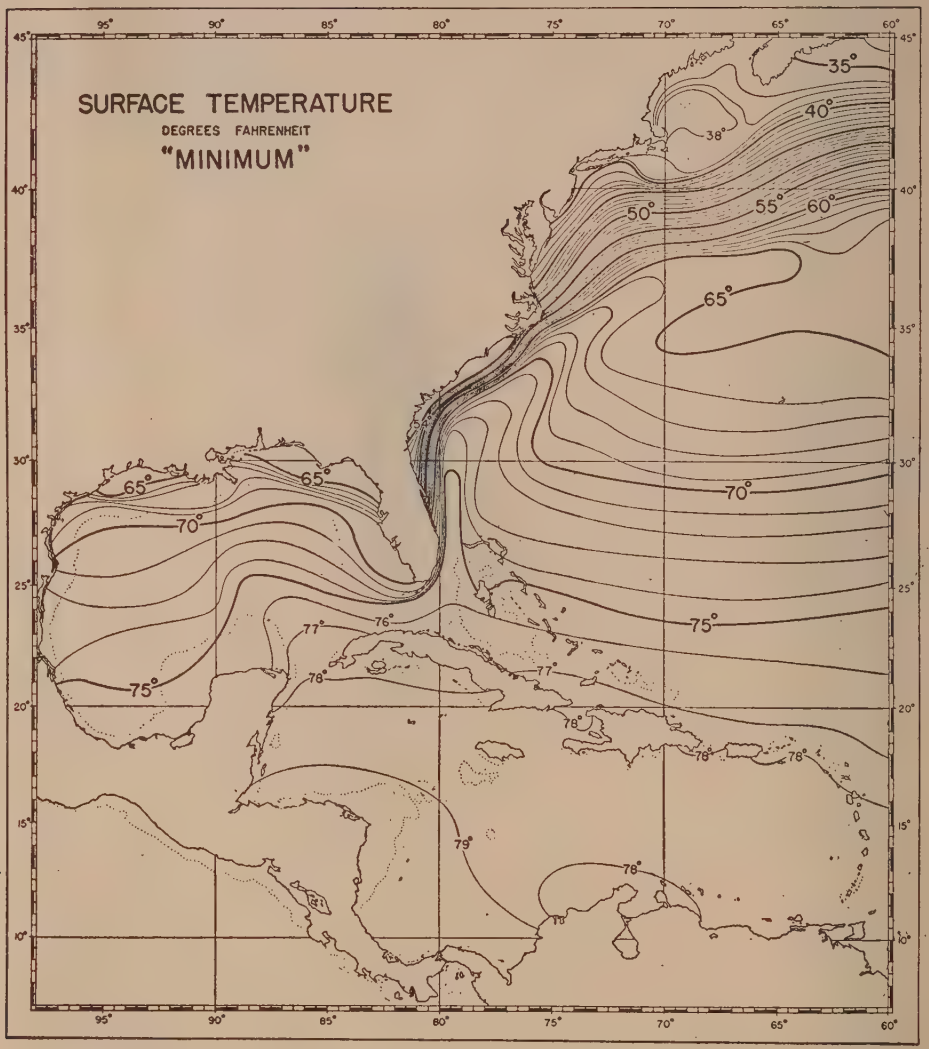

FIG. 8. Sea-surface isotherms for the mean Fahrenheit temperature of the coldest month (*isocrymes*) in the western Atlantic. From Fuglister ('47), Plate 14.

wrote, is thoroughly spoiled by the discovery of this species on the Atlantic coast from Beaufort to Florida and in Texas.

Such a difficulty of course does not strike at the validity of Hutchins' concept. If a species is found to have some other geographic limit than the one previously supposed, it is presumed that the limit is fixed by some other isothere or isocryme, and it is only necessary to redraw the map.

So far as the western Gulf of Mexico is concerned, Hutchins' scheme seems at first sight to provide a convincing explanation of the problem set in this paper. As shown in Figures 7 and 8, taken from Fuglister ('47, pls. 13, 14), the Gulf of Mexico is extremely warm in summer, but decidedly cool in winter. Figures 9,

10, and 11, based on records of the U. S. Coast and Geodetic Survey ('44), show the same features in a different way, and Figures 10 and 11 in particular give a better idea of the astonishing range of temperature experienced, not only seasonally, but from year to year. The mean monthly temperature at Galveston, for example, ranges from 14.3° C. in January to 30.7° C. in August, and temperatures as low as 1.5° C. and as high as 39.0° C. have been recorded in the 21 years of continuous daily observation. All the figures make it clear, moreover, that while the temperature regime is significantly more extreme in Texas waters than in northern Florida, the two regions are more similar to each other than either is to the region around Key West.

Variations of salinity are also extreme, both seasonally and geographically, along the Texas and Louisiana coast. It is impossible to do more than mention this fact in passing, however, for we have no idea of the variations actually encountered by the hydroids under consideration at the places where they are collected. Presumably, with the possible exception of the species actually taken on *Sargassum*, all the hydroids of the region are com-

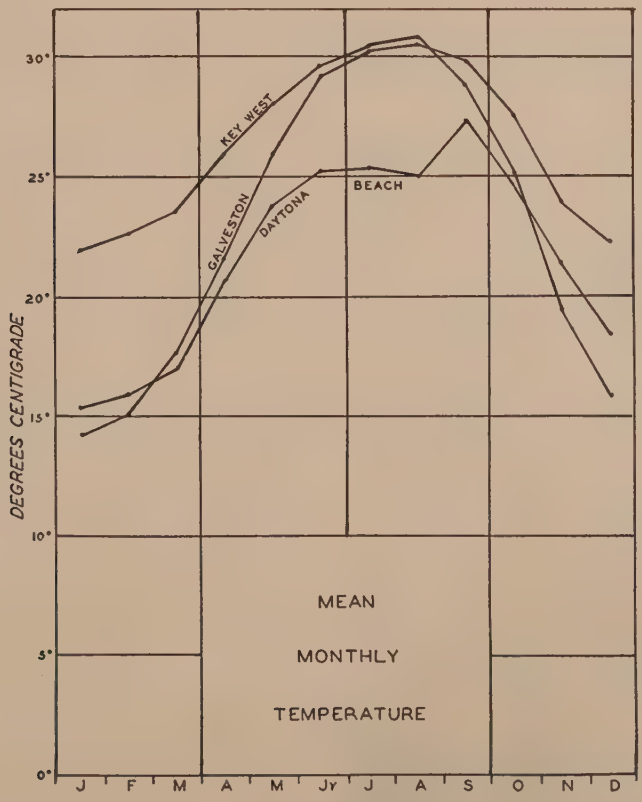

Fig. 9. Mean monthly temperature at Galveston, Texas, as observed by the U. S. Coast and Geodetic Survey, compared with that at Key West, in the Florida Keys, and Daytona Beach, on the Atlantic coast of northern Florida. The lengths of the records are: Galveston, 21 years, 1922–1942; Key West, 15 years, 1926–1940; Daytona Beach, 12 years, 1925–1932, 1939–1942.

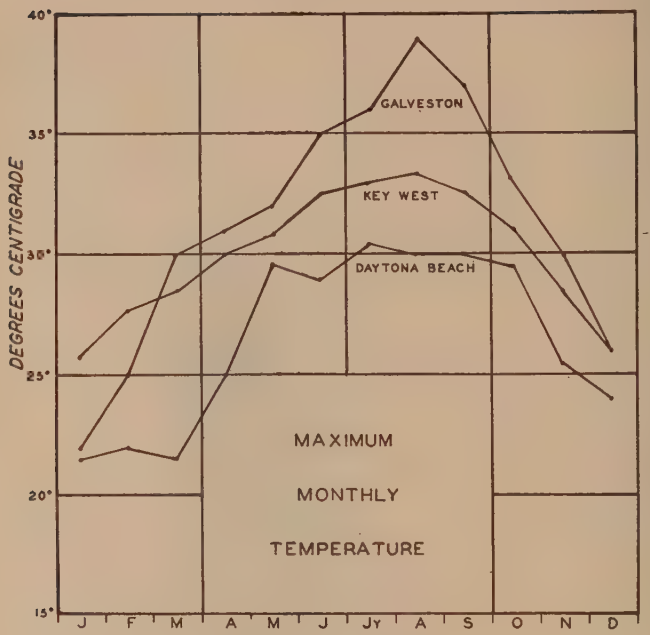

FIG. 10. Maximum temperature observed each month at the stations shown in figure 9.

paratively euryhaline as well as eurythermal, and this must have been an important factor in the survival of the boreal species in particular.

Neglecting salinity, and fixing attention solely on the temperature factor, then, one might predict that species of Types 2 and 4, with their equatorward limit set by the isocryme of 18° C., will have a markedly disjunct range, stopping at Cape Canaveral on the outer coast and reappearing in the vicinity of Pensacola and Galveston. Species of the same sorts, but which can breed when the temperature falls below 21° C., should stop at Palm Beach but would then be found almost everywhere in the northern Gulf; they might in fact be reported from Key West. Key West records would be rare, perhaps, for in the 15 years from 1926 through 1940 the mean January temperature there fell below 21° C. four times, but they might be frequent enough to give the impression of continuous range around the tip of Florida.

An explanation of this sort for the occurrence in Texas of such boreal hydroids as *Tubularia crocea* and *Podocoryne carnea,* however, cannot be complete, for it leaves untouched the question of the path of their migration from northern Florida to the western Gulf. *Obelia dichotoma* and *Cuspidella humilis* might well have gone around southern Florida, for the former is common at Key West and both have peripheral stations in equatorial waters. But there are reasons, discussed below, for believing that *Tubularia crocea* could not have done so under existing ecological conditions, and it would at least not violate conventional biogeographic practice to assume that the same applies to *Podocoryne carnea, Ectopleura grandis,* and the three species of *Bougainvillia.* This would be a dangerous assumption, since it depends on negative evidence, but if it be granted for the sake of argument it is clear that zonal typology by itself cannot explain real disjunctions of range, no matter how successful it may

be in accounting for continuous ranges along simple coastlines.

In making this point, which is the fundamental thesis of this paper, it is essential to make clear the distinction between Hutchins' zonal typology scheme and the whole suite of Hutchins' ideas of marine zoogeography. It is obvious from his remarks on northern relict populations in fjords ('47, p. 330) that Hutchins is well aware of the importance of historical factors underlying present distributions, and in private communications during several years he has emphasized the likelihood that the western Gulf of Mexico will be found to contain relict populations and endemic species. The antithesis between zonal typology and historical biogeography is deliberately set up, with apologies to Hutchins, as a device, a sort of straw man, because the former concept is open to a misinterpretation of the sort to which biogeographers are peculiarly prone. While Hutchins did not and would not say that existing ecological conditions are sufficient in themselves to account for ranges, the unwary or prejudiced reader of his too-brief paper might easily cite it in support of such a view.

There is only one hydroid on the list presented here which is well enough known to be profitably examined in the light of the zonal typology scheme. This is *Tubularia crocea* (Fig. 3), not only familiar as a source of embryological material at marine laboratories but of outstanding importance as a fouling organism. Close observation at Woods Hole (Sumner, Osburn, and Cole, '13), as well as laboratory experiments (Morse, '09;

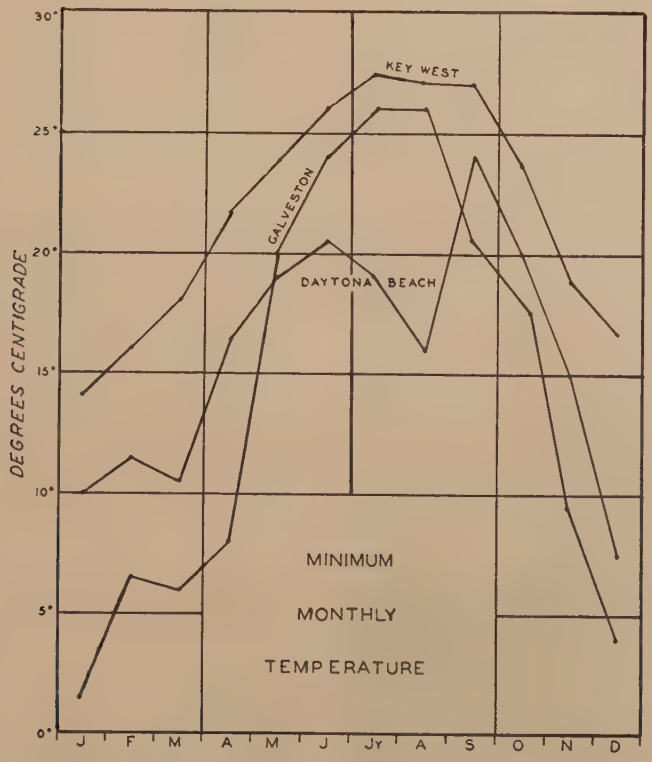

FIG. 11. Minimum temperature observed each month at the stations shown in figure 9.

Moore, '39), have shown that at temperatures above 20° or 21° C. the polyps die back into the stems, though they can regenerate at lower temperatures. The hydroid is found in flourishing (i.e. breeding) condition only in early and in late summer at this locality. North of Cape Cod, according to Morse, no such aestivation is found, and this is in agreement with the results of Fuller's ('46) experimental exposures of test panels at Lamoine, Maine, which showed the species attaching only in July, when the temperature is above 15° but below 20° C. At Beaufort the studies of McDougall ('43) leave no doubt that aestivation is protracted, and attachment takes place in April and again in November. If the *Tubularia* reported from test panels at Daytona Beach, Florida, by Richards and Clapp ('44) is *T. crocea,* as it probably is, it breeds at the southern limit of its range only in the winter, attachment taking place in October and November and aestivation beginning in May. The species is evidently absent entirely at Miami, for it never appeared as a fouling organism in Weiss's ('48) extensive studies there. Joel W. Hedgpeth reports (in a private communication) that the hydroid flourishes at Port Aransas only in the winter. On the Pacific coast breeding (again as determined by attachment to test panels) takes place in June at Oakland (Graham and Gay, '45), but in October at San Diego (Whedon, '43). All of this information points to a temperature of 20° or 21° C. as critical for aestivation, and one of about 10° C. for hibernation, though the latter figure is less reliable than the former.

Since the southern limit of the range in Florida is almost certainly at Palm Beach, where Fraser recorded a doubtful specimen, the agreement of the limit with the isocryme of 21° C. is precise. It is also a reasonable assumption that the species belongs to Type 2, the poleward limit being approximately fixed by the isothere of 12.8° C. (= 55° F.); a slightly higher isothere is in better agreement with the observed northern limits, for the species is not known so far north as Newfoundland or Glacier Bay, but the figure of 10° C. suggested by the data from test panels would require a lower isothere.

But if the northern limits of the species are determined in this way, and if the Florida and Texas occurrences are in entire agreement with expectation, what are we to say of the records of *T. crocea* at Jicaron Island, Panama, and in the Galapagos? The former, at least, is a strictly tropical locality, and the fact that both records are from a depth of 30 fathoms does not offer a very satisfactory explanation for the anomaly.

The observations and inferences as to the breeding season on the Atlantic coast strongly suggest that the hydroid known at Woods Hole, Beaufort, and Daytona Beach could not have reached Texas by way of southern Florida, where the waters are ordinarily too warm for it even in the coldest months. There appears to be no escape from the conclusion that historical factors have operated, along with mechanisms of the sort implied by the zonal typology theory, to produce the present range. In other words, *T. crocea* in Louisiana is to be regarded as a relict of a glacial age of the Pleistocene, when free migration of boreal species from the Atlantic to the Gulf coast was entirely practical.

This hypothesis rests on evidence much stronger than the range of *T. crocea* itself, as the following sections will show. But once it is admitted to apply to *T. crocea,* the occurrence of the species in the tropical eastern Pacific is understandable as a Pleistocene phenomenon of another sort: the Panama *Tubularia* must be a subspecies, physiologically different from the Atlantic coast form, and developed in isolation since the close of the glacial age that shifted the range of the species from the temperate eastern Pacific to what are now warm waters. Physiological subspecies are of course more difficult to detect than morphologically different forms, but there is no doubt that they exist; see

the work of Spärck ('36) on certain molluscs, for example.

It is legitimate to ask why an analogous physiological race of *T. crocea* has not developed in the tropical Atlantic. Such questions are always easier to ask than to answer. But it is a fact that certain species, widely distributed both in the Northern and Southern Hemispheres, are found to have more or less continuous ranges through the tropics on the eastern sides of oceans, but not on the western sides. Figure 4, showing the range of *Gonothyraea gracilis,* is an example. The significance of this pattern seems not to have been generally appreciated. It is a consequence of the general oceanic circulation that the subtropical regions near the sources of the westerly equatorial currents are cooler than regions of corresponding latitude on the opposite sides of the oceans. It should be easier, therefore, for a boreal or antiboreal species to cross the tropics on the eastern side, the distance between areas of adequately cool water being shorter. The crossing should have been easier during glacial ages than it is today. It is not definitely known that *T. crocea* crossed the Equator, the record from Valparaiso being no more and no less certain than the one from Luderitz Bay. But whether it did or not, it seems reasonable that it should have left a putative subspecies in the tropical Pacific but not in the tropical Atlantic.

The converse process, the spread of tropical species into temperate waters, has also proceeded farther along the eastern sides of oceans (see *Plumularia setacea,* Fig. 6). This, however, is not necessarily a Pleistocene phenomenon, but is more likely to be related to the fact that the annual temperature range is smaller in the eastern boreal regions than in the western. In particular, the winter temperatures are higher, and such species are presumably limited at their poleward boundaries by isocrymes.

The suggestion that physiologically different subspecies of familiar species may have evolved in favorable regions as a consequence of glacial and interglacial shifts of range implies another difficulty for the zonal typology concept. According to the theory, a boreal littoral species of a given type will have a different length of range, say, on the Atlantic coast of North America and on the Atlantic coast of Europe, but the northern and southern boundaries will be fixed by the same isotheres and isocrymes. But a species having so disjunct a range (and there are many of them, as discussed by Ekman, '35) will be subject to the evolutionary divergence that ordinarily accompanies geographic isolation, and physiological differentiation is just as likely to ensue as is morphological separation. So if any large number of such species are found to be limited in their meridional spread by precisely the same physiological mechanism, this can only be because the time elapsed since their isolation (say since the last interglacial age, when the eastern and western populations were continuous across the North Atlantic) has been too short for significant differences in physiology to arise. Fortunately for the paleoclimatologist, the rate of evolution and speciation in most marine invertebrate groups appears to be low (Simpson, '44); otherwise one might be more pessimitic concerning Hutchins' suggestion ('47, p. 334) that "by studying the fossil distributions of selected series of forms, it should be possible to map the distribution of maximum and minimum monthly mean temperatures for earlier oceans."

In short, Hutchins' system of zonal typology, though admirably conceived and certain to be of great use to the marine biogeographer, cannot stand alone, nor did its author intend that it should. Historical changes of ecology have also had their effect, and when the distribution of species and subspecies (rather than of genera and higher categories) is being discussed, Pleistocene changes of sea temperature will have to be considered before more ancient geographic conditions are called into account. Where such changes have operated to produce relicts and dis-

junctions of distribution on the one hand, and clandestine physiological speciation on the other, the difficulty of applying zonal typology will be formidable.

Other Gulf coast disjunct distributions

There is no biogeographic significance in the fact that all but one of the hydroids reported here are new records for Texas. Nor, probably, is it particularly significant that of the nine new records from the Gulf of Mexico (excluding the doubtfully identified *Eudendrium tenue*), six species are extratropical, do not occur at the Tortugas or Key West, and therefore might not have been expected in the western Gulf. Their disjunction from the boreal Atlantic range is certainly significant, but the proportion that they make of the total fauna is not; if hydroids had been collected systematically from this region before, the problem would merely have been recognized sooner, whereas future collecting may turn up a much larger number of strictly tropical species without affecting the argument. It is necessary to ask, however, whether hydroids are exceptional or perhaps unique among marine organisms in having an appreciable number of boreal disjuncts.

This is not an easy question to answer, in view of our inadequate knowledge of the ranges of some of our commonest littoral species, and our almost complete ignorance of the fauna of the western Gulf. For very few groups have competent systematists reviewed the records for the entire Atlantic coast of North America, and for the non-specialist to scrutinize the monographs that are available, none of which were written with the needs of the biogeographer in mind, is to run the risk of making egregious misjudgments. Enough can be learned by this procedure, nevertheless, to suggest that the problem of boreal disjunction is at least not entirely peculiar to hydroids.

Rathbun's monographs on certain families of crabs ('18, '25, '30, '37) offer the most logical starting point, and it is immediately apparent that not many crabs show the distribution pattern of such Texas hydroids as *Tubularia crocea*. It is exasperatingly frequent in other taxonomic works to find ranges stated extremely broadly—"Labrador to Yucatan," "Cape Cod to Brazil," *etc.* Such ranges, when stated by Rathbun, however, are almost invariably thoroughly documented by records from the wonderfully rich collections of the U. S. National Museum. In all of the four volumes I have found only five species whose ranges suggest boreal disjunction on the Texas or Louisiana coast, yet the fact that many crabs have really been collected in Texas, and the wealth of data for the other species, give one confidence that some of these cases are genuine, and not the result of inadequate collecting. They are the grapsoids *Dissodactylus mellitae, Sesarma reticulatum, Uca minax* and *U. pugnax* (see Rathbun, '18) and the cancroid *Rhithropanopeus harrisii* (see Rathbun, '30). One of these species, *Uca pugnax,* has a tropical subspecies occurring at Matagorda, Texas, and so is probably not fairly included. Another, *Rhithropanopeus harrisii,* is represented in the Woods Hole collection by specimens from San Francisco Bay (Georgiana B. Deevey, MS in preparation), and may be distributed as a fouling organism. If crabs as a group are not very favorable for the detection of Pleistocene relict distributions, possibly the reason is that most of the species are older than the Pleistocene.

It is unfortunate that the molluscs of the Atlantic and Gulf coasts have not been critically reviewed by a modern author. Revisions of certain genera and families have been published in *Johnsonia,* but there is still no reliable guide to the distribution of the group as a whole. Probably the best case of boreal disjunction is that of *Littorina irrorata* (see Bequaert, '43), which evidently does not occur in eastern Florida south of Indian River, but reappears at Charlotte Harbor on the west coast and then extends to Point Isabel, Texas. Examination of Smith's

('45) list, a more complete but less authoritative compilation than the papers of Clench, Bequaert, and their colleagues, suggests that boreal disjunct patterns are common among molluscs, perhaps as common as among hydroids. For example, at least three of the species well known as Pleistocene fossils on the Gulf coast are absent from southern Florida: *Abra aequalis, Rangia cuneata,* and *Dentalium texasiana.* And, as Mr. Hedgpeth has pointed out (in correspondence), the commercial oyster, *Ostrea virginica,* though recorded from the tropics, is common enough to be economically important only on the Atlantic and Gulf coasts.

Fishes, like molluscs, have not been collected systematically enough in the United States to establish patterns of distribution for the group as a whole. Certain recent revisions of genera and families, taken more or less at random, however, make it clear that boreal disjunctions are not lacking. Thus the anchovy *Anchoa mitchilli* (see Hildebrand, '43) is unknown from the Florida Keys and the West Indies. The type subspecies ranges from Massachusetts to North Carolina. From Delaware Bay southward it may overlap the range of the southern subspecies, *A. m. diaphana,* which follows the Gulf coast to Yucatan. Other examples, drawn from among the gobies, are *Gobionellus shufeldti* (see Ginsburg, '32) and *Gobiosoma bosci* (see Ginsburg, '33).

The commercial shrimp, *Penaeus setiferus,* is a possible example of boreal disjunction; Burkenroad ('39) gave its range as "Atlantic coast of the United States from Fire Island, New York, to Cape Canaveral, Florida; Gulf of Mexico from Pensacola, Florida, to Timbalier Bay, Louisiana, Texas, and Vera Cruz, Mexico; Cuba; Jamaica," and remarked that the absence of the species and of the subgenus to which it belongs from southern Florida is almost certainly real. The distribution of the littoral Penaeidae has many pecularities, however, no doubt because of their rather wide bathymetric range and migratory habit, and the absence of the shrimp from southern Florida is more probably the result of the lack of suitable habitats there.

Boreal species that are absent from southern Florida and reappear in the northern or western Gulf of Mexico are thus shown to be not infrequent among other groups of marine animals than hydroids. It is not an essential part of the theory that interprets them as relicts of a glacial age of the Pleistocene that a high proportion of species should show this pattern, a "reasonable" number being all that is required by a critical biogeographer. The actual proportion might be higher, however, if genera rather than species could be taken into consideration. That is, there may be species that are for the most part endemic to the western Gulf, developed from ancestors isolated there since a glacial age. By convention, a greater antiquity would be assigned to such isolation than to one that had merely left a separate population of a species known elsewhere. This kind of argument is so greatly affected by variations in taxonomic practice, both within and between groups, that it is best not employed for marine organisms. Moreover, it is obvious that if an endemic species, developed, say, since the Kansan glacial age, had changed its ecological requirements during the ensuing ages and begun to spread from the Gulf of Mexico in postglacial time, it would be difficult to distinguish it from a tropical American species (like *Clytia fragilis*) which might have had a different origin. For these reasons the subject of Gulf of Mexico endemism will be dismissed with the remark that there are no endemic species on the list of hydroids from Louisiana and Texas, unless *Bougainvillia inaequalis* is a good species. A clear case of endemism occurs among the silversides (*Menidia*), and was discussed in a recent paper by Gosline ('48), but this is an instance of invasion of brackish water by a marine fish and may not be a Pleistocene phenomenon.

There remain for consideration two important points, bearing somewhat more

remotely on the biogeography of the western Gulf. One is that those Texas fishes that breed in the fall and winter are predominantly of more northern distribution than the larger group of summer spawners (Gunter, '45); this recalls the case of *Tubularia crocea.* The other is that the western Gulf is not the only place where boreal relicts occur in comparatively warm waters, for the northern shores of the Mediterranean (Ekman, '35) harbor a number of such species. The occurrence in the northern Adriatic of the hagfish, *Myxine glutinosa,* and the plaice, *Pleuronectes platessa,* is of particular interest, but the cases of *Podocoryne carnea* and *Hydractinia echinata* (Fig. 2) should be noted. Boreal relicts are also represented among the fishes of the northern Gulf of California (Hubbs, '48).

The marine Pleistocene of the Gulf coast

It is difficult to obtain a picture of the Pleistocene of the Gulf coast that has any particular relevance to biogeography. From the standpoint of stratigraphy there is little to differentiate Pleistocene formations from those of the earlier Cenozoic, and while the subsurface geology of the region has been extensively studied by petroleum geologists, Pleistocene deposits have received only a small share of this attention. Much of the material composing them is the result of alluviation on a grand scale, and it is clear that the Gulf shoreline has moved back and forth during Pleistocene time as it did throughout the history of the coastal plain. There is no general agreement, however, on age relations within the Pleistocene, and few formations are definitely known to be either glacial or interglacial.

The outermost and topographically lowest parts of the coastal plain have Pleistocene deposits at the surface, and outcrops of successively older formations are encountered in going inland. Nearly all the Cenozoic beds dip in a general way toward the Gulf and pass beneath younger materials, increasing in thickness as they do so, so that the total thickness of Cenozoic sediments at the shore of the present Gulf is greater, probably much greater, than 10,000 feet. Difficulties in correlation, especially in identifying horizons in borings, arise from three important circumstances: (1) the deposits are generally unfossiliferous, particularly at their landward edges; (2) much of the dip is the result of downwarping of the crust beneath the sediments since their deposition, and the downwarping was not regionally uniform throughout Cenozoic or even throughout Pleistocene time, but directed toward the locality of maximum overburden by sediments; (3) in certain places salt domes have punched into the sediments from below, compressing and contorting them.

The leading idea in the Pleistocene stratigraphy of the Gulf coast is that of glacial control of sea level: cycles of alluviation and erosion have alternated rather regularly, alluviation occurring during times of high or rising sea level (interglacial ages), while erosion was predominant during times of low or falling sea level (glacial ages). Biologists in particular must be warned, however, that this idea is not so simple in its application as it appears. As the Pleistocene formations are ordinarily flat-lying, each one being separated from the next older by a more or less well defined scarp, it has been thought, notably by Cooke ('30, '35), that several shorelines of interglacial age are represented by their respective "terraces." Few of the scarps, however, are demonstrably wave-cut benches, and only the lowest "terrace" carries marine fossils, the maximum elevation of which is about 25 feet above sea level everywhere from New Jersey to Texas (MacClintock and Richards, '36; Richards, '36, '38a, '39a, '39b). Most workers therefore believe that the higher scarps are not wave-cut and the higher "terraces" not erosional, but constructional. The formations are believed to be mainly deltaic near their landward edges, merging laterally into a "deltaic coastal plain" (Bar-

ton, '30a, '30b), now more or less dissected, and grading down dip into seafloor sediments, now mostly covered by the sea or by younger sediments. The impression of terraces is commonly explained as the result of tilting of the strata down toward the Gulf and toward the axis of the Mississippi embayment, where the mass of sediment has overloaded the crust most heavily (Russell, '40; Storm, '45). The amount of tilting has been greatest for the oldest formations and the youngest deposits therefore lie almost horizontally against scarps formed where the older beds dip underneath them.

This interpretation is not in conflict with the hypothesis of glacial control, but it eliminates the present altitude of a "terrace" scarp as evidence for the height of an interglacial sea. Thus it is impossible to determine a sequence of sea levels from a series of scarps visible on a topographic map. It is still possible to make use of stream terraces, some of which seem to grade into coastal formations of terrace aspect (Fisk, '38a, '38b), as evidence for high sea levels of the Pleistocene. And it is still possible to follow Pleistocene formations in the direction of their dip as they appear in well borings beyond the limits of their outcrop. But the difficulties stated above are great, and Frink's attempt ('41) to apply glacial control in systematic fashion to the subsurface Pleistocene of Louisiana is rightly rejected by Lucke ('41) as uncritical.

It is against this background of inadequate data and faulty interpretation that Richards' contributions to the marine Pleistocene must be assessed. Marine fossils are confined to deposits underlying the youngest and lowest "terrace" of the entire coastal plain. The list of molluscs found or critically revised by Richards in his various papers is a long one, including several hundred species. Most of them are poor ecological indicators, for it is an unfortunate fact that the seasonal temperature range along the Atlantic coast of the United States is so wide (as compared with that of Europe or the Pacific coast, for example) that none but eurythermal species are likely to occur there, and this is true in even higher degree for the Gulf coast. Thus it is not surprising that the Pleistocene fauna taken collectively differs very little from that of the same region today. It includes the same extraordinary mixture of temperate and tropical elements (using these terms in the recommended indefinite sense), and the most that can safely be said of a collection including *Mulinia lateralis* and *Modulus modulus, Polinices duplicata* and *Murex fulvescens,* is that it is not arctic. At a few places, notably at Delray, near Palm Beach, Florida (Richards, '38a, p. 1276), a fair number of fossils belong to species now confined to more southern waters. Occasionally a northern animal has been reported, but one of the most striking of these, the barnacle *Balanus crenatus,* is listed from southern North Carolina without comment by Richards ('36, p. 1647).

Because of the nonglacial character of the fauna of the lowest terrace, variously called Cape May, Pamlico, Anastasia, Port Hickey, and Beaumont, and because the marine fossils occur up to an elevation of 25 feet above sea level, Richards concluded that these formations are all essentially the same, and that they are of interglacial age, probably last interglacial or Sangamon. So large a proportion of the shells come from borings, however, that it would be astonishing if errors in stratigraphy have been avoided, and the molluscan fossils are hardly likely to be all of the same age, even if they are all interglacial. The possibility that the Palm Beach warm fauna, which came from a depth of 118 feet in a well, might belong to an earlier interglacial than the last was recognized by Richards. In Louisiana, on the other hand, fossils occurring as deep as 2,470 feet below sea level are considered to be possibly of Pamlico-Beaumont age, having been caught in the downwarping and covered by post-Sangamon Mississippi sediments. The validity of this conclusion and of

many others like it cannot be proved until a thorough stratigraphic study is made of the Pleistocene of the entire Gulf coastal plain. Meanwhile taxonomists, especially malacologists, should survey the modern fauna of the Gulf of Mexico, so that biogeographers can determine what is really meant by the statement, almost grotesquely ambiguous in the light of the present study of the hydroids, that "the Pleistocene species are living in the same region today."

The known marine molluscs of the Pleistocene Gulf of Mexico, then, are probably of interglacial age and quite possibly of several interglacial ages. Few species and no whole faunas suggest the cool conditions that must have prevailed during glacial ages, and nothing in Richards' work bears directly on the problem of boreal disjunction among hydroids, though it is useful to know that extreme environmental variation has been typical of the waters of the Gulf of Mexico for a long time.

Evidently the glacial ages are represented in stratigraphic sections, not by fossiliferous marine deposits, but by nondiagnostic sands and gravels or by erosional unconformities. It will take close study to demonstrate these stages in localities near the present seacoast. For evidence that they played their part in the Pleistocene history of the region it is necessary to turn to the analysis of submarine cores taken in deep water. This work has barely begun, but Trask, Phleger, and Stetson ('47) have studied some of the many cores collected in the Gulf by the "Atlantis." They reported that one core, the only one so far examined for Foraminifera, shows a subtropical fauna at the surface, grading downward into one called "definitely sub-arctic." More recently, Phleger ('48) investigated a long core taken by the "Albatross" in the Caribbean in Lat. 14° 25′ N., and found 11 layers containing cold-water Foraminifera, including some regarded as "arctic." It must be emphasized that these species of Foraminifera are pelagic, for of course the depths at which they are fossilized are extremely cold today. Such results are challenging; in fact they raise the uncomfortable question, "what happened to the genuinely tropical fauna during glacial ages of the Pleistocene?"

Terrestrial and fresh-water Pleistocene fossils are not unknown in the Gulf States, and they also have a bearing, though a somewhat more remote one, on marine biogeography. Of outstanding importance are the remains of flowering plants, mosses, and fresh-water molluscs found in the Port Hickey deposits along Little Bayou Sara, Louisiana (Fisk, '38b; Richards, '38b; Brown, '38; Steere, '38). Among the trees are white spruce, larch, and arbor vitae, while northern species were also found among the molluscs and mosses. The northern types occurred together with plants and animals still living in the region, a fact that would not stand in the way of a glacial dating, for intermingling of northern and southern elements is what one would expect to find in Louisiana during glacial ages. Fisk ('38b) correlated the Port Hickey formation, which underlies the lowest "terrace" in the region, with the Peorian interval. He pointed out that the fossils came from the lower part of the formation, and believed that the Port Hickey episode of alluviation was related to a rising sea level, but that during the early part of the rise, from a low stand during Iowan (early Wisconsin, glacial) time, conditions were still essentially those of a glacial age. Though the conclusion is reasonable, the dating seems to lean too heavily on the ideas of Cooke, for deglaciation during the Peorian interval is believed to have been insufficient to have resulted in a major rise of sea level (Flint, '47). It is more likely that the fossils are of early Sangamon age.

The other examples of northern species found as fossils in the southern States are even less satisfactory, stratigraphically, than those of Little Bayou Sara. They make it clear, however, that decidedly cool climates prevailed at times during

the Pleistocene as far south as the present Gulf coast. Remains of larch, for instance, have been found in Pleistocene deposits of uncertain age near Dahlonega, Georgia (Eckel and Kelly, '36; Richards, '36). In various parts of Florida freshwater peat containing cold-water diatoms overlies brackish-water deposits referred to the Pamlico or Anastasia stage (Gunter and Ponton, '33; Hanna, '33). It is not clear whether this peat represents the same time interval as the peaty material found under many Florida mangrove swamps by Davis ('40), or the Van Valkenburg bed overlying the Melbourne bone bed at Vero, which in turn overlies the Anastasia.

The controversial problem of the Vero deposits, in which remains of "early man" were found, has recently been reviewed in comprehensive fashion by Rouse (MS, to be published in *Yale University Publications in Anthropology*). Rouse points out that the latest movement of the sea level along the coast of eastern Florida is a rise, and correlates this with a rise of water table at localities some distance back from the coast, especially in the Indian River area. These events are clearly recent, i.e. postglacial, but the formation of the Melbourne bone bed probably dates from late Wisconsin or early postglacial time, and so, presumably, does that of the cold-water peat. Pollen of spruce and fir has been found in buried Pleistocene peat in borings made along the course of the proposed Cross-Florida Barge Canal (Davis, '46), but as marine deposits overlie the peat here it is probable that the glacial age represented is earlier than Wisconsin.

Only a handful of pollen profiles have yet been obtained south of the glacial boundary. It is noteworthy, however, that all but one of them (the one from Dismal Swamp, Virginia) show spruce and fir pollen at their bases (Deevey, '49). The cool-climate pollen zones may not all be contemporaneous, and some of the pollen may have been wind-borne from a considerable distance, but the occurrence of fir pollen in Texas is most difficult to explain away on this basis.

Regardless of the negative evidence from marine deposits, therefore, it is beyond doubt that glacial climates of the Pleistocene have made themselves felt in the southern States. As a result the waters of the Gulf of Mexico must have been appreciably colder at all seasons, but particularly in summer, than they are today. No great drop in sea-surface temperature in the vicinity of the Florida Keys would be necessary to account for the finding of boreal relicts along the Texas and Louisiana coast. Evidence from modern biogeography is never very precise, and could not be expected to point to the prevalence of arctic conditions in a region that is now essentially subtropical. Probably a lowering of the mean annual temperature at Key West by 5° C. (bringing it down to the figure for Daytona Beach) would suffice to explain all the Texas disjunctions. But this is a greater lowering than is suggested by any other *marine* evidence except that of the foraminiferan assemblages in submarine cores; the latter data are so unexpected that they stand in need of all the confirmation that the biogeographic and all other approaches can provide.

Conclusion

The hydroid fauna of Texas and Louisiana, so far as it is now known, is dominated numerically by tropical and subtropical species. This would be expected in view of the high temperatures found throughout the Gulf of Mexico in summer, the direct continuity of hydroid habitat between the northwestern Gulf and the strictly tropical waters farther south, and the repeated opportunity for introduction of these sessile organisms on *Sargassum* and other tropical flotsam. A significant proportion of species, however, are of boreal rather than tropical distribution, and their ranges present a remarkable pattern of disjunction, the boreal section having its limits at Beaufort, Day-

tona Beach, Cape Canaveral, or Palm Beach.

Ecological variation in the western Gulf is so extreme, both seasonally and geographically, that it is not surprising to find there a mixture of faunas that would be almost incredible anywhere else. Such a mixture could in fact be predicted from a careful analysis of present-day conditions, temperatures especially, provided such an analysis looks beyond the generalized averages and takes annual ranges into consideration. Thus the zonal typology scheme of Hutchins, which starts with the reasonable assumption that temperature is the most important single influence on marine biogeography, offers an explanation for the continued existence of certain boreal species side by side with tropical species in Texas and Louisiana.

But no theoretical scheme that confines its attention to present-day distribution of ecological factors can give a complete explanation of geographic patterns. Historical factors have also operated. The ecology of the oceans has changed radically within the geologic life span of most of the species existing today. Since most modern species can safely be assumed to have arisen since the beginning of the Pleistocene, it is obvious that they have experienced wholesale modifications of range as a result of alternating shifts from glacial to interglacial climates and back again. The present ocean is essentially interglacial in character, but glacial conditions prevailed as recently as about 25,000 years ago.

Barriers opposing the dispersal of littoral marine organisms under the present climatic regime, such as the existence of high winter temperatures in the vicinity of the Florida Keys, are certainly of postglacial origin. The boreal hydroids and other organisms of the Texas and Louisiana coast are therefore interpreted as relicts of a glacial age of the Pleistocene. They are species whose ranges in glacial (probably Wisconsin) time were continuous through the glacial-age counterpart of the present boreal zone. Presumably they are few in number because only a fraction of the boreal animals were sufficiently tolerant of seasonal changes of temperature (and sufficiently euryhaline as well) to survive in the extreme environment of the western Gulf during all of its postglacial history.

Summary

Examination of two small collections of marine hydroids, mostly from Texas, has yielded results of interest quite out of proportion to the size of the collections and the number of species identified. None of the species is new, and the fact that all but one of the 26 are new records for Texas merely reflects an almost complete lack of previous collecting. A total of 39 hydroids are now known from Louisiana and Texas, but it cannot yet be decided whether this small number means that the fauna is impoverished.

The exceptional interest of the new records lies in their zoogeographic implications. Of the nine or ten species newly recorded for the Gulf of Mexico, six or seven are more or less distinctly boreal in distribution, and seem out of place in a fauna so largely dominated by subtropical elements, including many *Sargassum*-borne species. Those that look most remarkable on a distribution map are *Podocoryne carnea* (Fig. 2) and *Hydractinia echinata*, but the case of *Tubularia crocea* is most satisfactory, for there is good reason to believe that the species is really absent from southern Florida, and there is experimental evidence that it could not live there.

The boreal disjunct distribution pattern, in which the main American range of the species is broken into two parts by the peninsula of Florida, is shown not to be entirely peculiar to hydroids, though it is impossible to say how general it may be.

It is supposed that the western Gulf populations of such species are relicts of

a glacial age of the Pleistocene, the most eurythermal (and euryhaline) survivors from a time when high winter temperatures did not form a barrier in the vicinity of Key West. The annual temperature range in the western Gulf is wider than in almost any other part of the ocean today, and the resulting mixture of boreal and tropical elements of the marine fauna was also characteristic of interglacial ages. It is shown that the *zonal typology* scheme of Hutchins, according to which species are limited in four different ways by combinations of maximum and minimum temperatures (represented on distribution maps by isotheres and isocrymes), accounts for the continued existence of the boreal species along the northern shore of the Gulf. But no analysis of present-day ecological conditions can explain fully the crossing of barriers by marine animals.

Our scattered and confusing knowledge of the Pleistocene geography of the Gulf States is briefly reviewed, and it is found that the only valid marine fossils of glacial age yet reported are the cold and arctic assemblages of Foraminifera in submarine cores. The marine molluscs of Pleistocene formations accessible from the land are evidently all of interglacial age, though cool conditions of glacial ages can safely be inferred from fossil land plants and fresh-water molluscs. The pertinent fossil evidence (white spruce, larch, and arbor vitae in Louisiana, pollen of spruce and fir in Florida and Texas, etc.) points to cool climates, probably to much cooler summers than those of today, but does not go nearly so far as the Foraminifera in implying arctic or subarctic conditions. The zoogeographic evidence of boreal disjunction requires a glacial lowering of the mean annual temperature at Key West by at least 5° C., but this is a minimum estimate. The limitations of the biogeographic method are such that stronger testimony of glacial climates cannot be expected, and there is no conflict between views based on this estimate and on the arctic Foraminifera.

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FLORA OF GUATEMALA

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The flora of Guatemala (Standley and Steyermark '45, Smith 1889–1907) is the richest and most diversified of any in Central America for a variety of reasons. This is due not only to a combination of varied climatic, physiographic, and edaphic conditions, but also to a long and diverse geological history. Extremes range from hot deserts, seashores, and lowland rain forests to cool temperate oak-pine, fir, or cupressus forests, moist cloud forests, alpine meadows, and volcanic summits; temperatures range from 16° F in the highlands to around 100° F in the Motagua desert; altitudes vary between sea-level and 4,210 meters on the summit of Volcan de Tajumulco; rainfall from 6 inches to 200 inches annually, and varying from a dry season of half a year to almost daily rains throughout the year; topographic features range through plains and everglade-like country, mountain lakes, sulfur fumaroles and springs, waterfalls, steep canyons, caves, clear spring-fed mountain streams to dark brown waters of lowland areas, and rocks varying from limestones and sandstones to marbles, serpentine, gneisses and mica-schists to granites, diorites, pumice, basalt, and volcanic ash (Griscom '32).

The 14 major volcanoes are all of Pleistocene and Recent origin. The present limestone plains and hills of Petén in northern Guatemala resulted from the marine inundations of Tertiary times (Schuchert '35). But the most interesting parts of Guatemala are the old mountains of the southern part (fig. 1) that extend in an east-west direction from the Sierra de los Cuchumatanes to the Sierra de Chuacus and Sierra de las Minas. These mountains, formed of Paleozoic and Mesozoic rocks, are part of an ancient nuclear core of Central America (Sapper 1894), and have been available for plant occupation since the end of the Cretaceous period. Many genera whose ancestry dates back to late Cretaceous and early Tertiary times occur only in this area of ancient strata. The family Magnoliaceae, of proved ancient lineage, and occurring at present in eastern Asia and eastern North America as well as in Central and South America, is represented in Guatemala by the genera *Magnolia, Talauma,* and *Drimys,* which occur in Guatemala only on these old strata. Likewise, are found *Osmunda, Ceratozamia, Taxodium, Taxus, Juniperus, Podocarpus, Carpinus, Juglans, Alfaroa, Distylium, Liquidambar, Matudaea, Platanus, Acer, Sarcococca,* and *Befaria*—and all limited to these older rocks. None of these or similar groups are found on the youthful slopes of the volcanoes formed in Pleistocene times, or on the Tertiary lowlands of Petén, or on the Pleistocene formations of the lowlands of Izabal or the Pacific bocacosta. Just as some genera in the United States, such as *Cladrastis, Cotinus,* and others, are represented by fossil ancestors which prove their existence back to late Cretaceous or early Tertiary times, and now are confined to the old Appalachian-Ozark plateau, which has been available for plant occupation since the end of the Paleozoic era, so do similar examples in Guatemala point to anciently distrib uted types.

Upon this area of old rocks are found some of the most remarkable genera endemic to Guatemala, such as *Tintinnabularia* and *Guamatela.* To this area are restricted such peculiarly isolated species as *Mitchella repens, Gelsemium sempervirens, Parthenocissus quinquefolia, Rhus radicans,* and *Berchemia scandens,* otherwise known only from the United States and northern Mexico. The remarkable parasite, *Mitrastemon,* is also found in the area of older strata.

Likewise, the greater variety of the

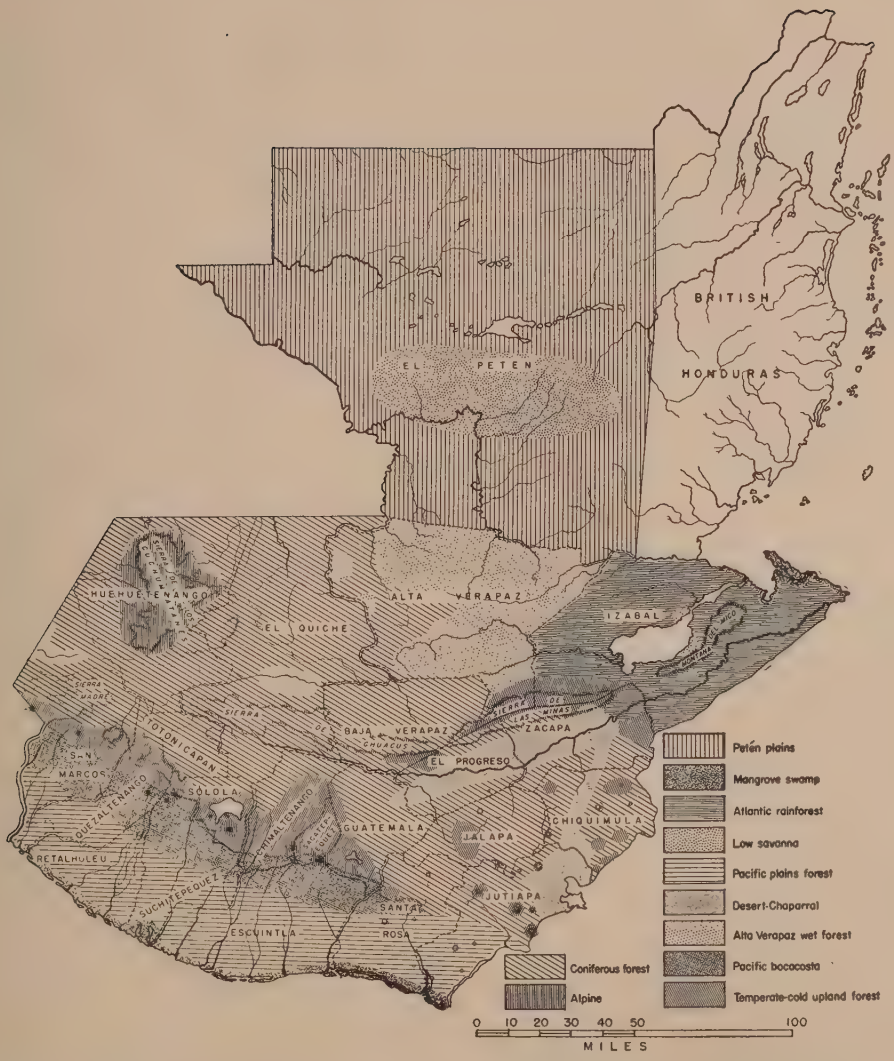

FIG. 1. Map of Guatemala showing vegetation regions, and important topographic features. Data on vegetation from Lundell ('37), Popenoe ('26), and Rodriguez ('21).

alpine flora in Guatemala is mostly confined to the ancient Sierra de los Cuchumatanes, whose cool summits have been available for occupation by the land flora since early Tertiary times, following the period of late Cretaceous marine deposits and subsequent mountain making. Only a small part of this alpine flora is preserved on the summits of the more youthful volcanoes. The alpine summit flora of these volcanoes apparently has been derived from the more ancient flora of the Sierra de los Cuchumatanes, which was in existence long before the Pleistocene-born volcanoes came into being. Many endemic genera and species restricted to the volcanic region of Guatemala apparently owe their existence to geographic isolation induced after the volcanoes were formed.

Due to its marine flooding by Tertiary

seas, what is now Petén was not available to plant occupation until late Pliocene and early Pleistocene times. Its flora arrived from the rest of the Yucatan Peninsula, of which Petén is a part, and from the lowlands of British Honduras, Izabal, and northern Alta Verapaz. For this reason, the Petén flora is mostly unlike that of the older mountain mass of Guatemala, and, therefore, none of the genera of ancient lineage, previously referred to, are found in Petén.

Although many genera found in Guatemala are common to South America (Bartlett '35), it may be stated that the flora is conspicuously a Mexican one, especially of southern Mexico. In other words, most of the genera of Guatemala can also be found in some part of Mexico. Particularly obvious in exhibiting this Mexican affinity are the pine-oak forests, which are so common throughout the highlands and mountain slopes. The pine and oak forests of Guatemala resemble in general appearance those of the southern Rocky Mountains, especially those of New Mexico. There is the same general effect of spaced pine trees sheltering ground covered with low grasses and herbs, and the appearance of the herbaceous plants is similar in both regions, even to the possession of the same genera, such as *Aristida, Andropogon, Bouteloua, Arenaria, Ranunculus, Agrimonia, Potentilla, Lupinus, Cologania, Dalea, Linum, Penstemon, Castilleja, Stevia,* and many others.

A few South American elements, such as *Plantago tubulosa, Alchemilla pinnata, Werneria nubigena, Bidens triplinervia* var. *macrantha, Aphanactis,* and *Crumenaria,* which reappear in Guatemala, indicate survivors of an earlier once continuous land mass connecting Central and South America, and accentuate the antiquity of the now disrupted floras. On the other hand, the South American floral elements found in the rain forest of the North Coast of Guatemala are of a type having a wide distribution, from Veracruz and the Isthmus of Tehuantepec, southward along the whole Central American coast into Colombia. They are of the same type that in South America extend southward to most parts of the Amazon Valley. Most genera of trees of this rainforest, as represented in Central America, occur also in the Amazonian forest, and many tree species extend throughout this whole area. Similarly, the type of vegetation prevailing along the Pacific coast of Guatemala is of wide distribution in tropical America. It follows the Pacific as far north as Sinaloa, Mexico, and southward into western Panama. This same type of vegetation is widely developed also on the north coast of South America, in Venezuela and Colombia. Therefore, it may be stated that even though the flora of Guatemala is conspicuously a southern Mexican type, it partakes also of a South American quality, especially in those areas of the north coast rainforest and the Pacific bocacosta where the South American genera have penetrated northward and are contiguous to the regions of Central America and southern Mexico, largely connected with one another by the continuously distributed Quarternary and Recent formations extending between these regions.

Finally, I wish to speak about the remarkable relationship shown in the flora of Guatemala with that of the United States. It is a most striking relationship and may be explained upon geological grounds. This relationship is two-fold, (1) consisting of species related to the flora of the eastern United States, and (2) of those related to the flora of the Rocky Mountains or southwestern United States. Let us examine first the relationship of the flora of Guatemala with that of the eastern United States. Fernald has shown that the Coastal Plain flora of Atlantic North America possesses many elements belonging to otherwise tropical groups, and that these were apparently descended from plants which during Cretaceous times occurred on the low-lying Appalachian area, which became the uplifted Appalachian Plateau during Ter-

tiary times. Many of these tropical groups besides being represented today on the Appalachian Upland are found also on the high tablelands of Mexico and Central America, or at other places back of and older than the Outer Coastal Plain. Since the Appalachian Upland, like the Ozark Plateau, is known to have been unglaciated and uninvaded by seas since the end of the Paleozoic era, and the oldest areas available for plant occupation, the flora confined to these plateaus is considered to be of as ancient ancestry as any now living in eastern North America. It is equally logical to state that the Coastal Plain groups, derived from the ancestral Appalachian peneplain, belong to this ancient distribution. A large number of these last remnants of the ancient floras have migrated from the old Appalachian and Ozark plateaus into the Coastal Plain. Examples of these are *Liquidambar, Taxodium,* and *Berchemia,* all of which are found in Guatemala as well as on the Coastal Plain of the United States and in parts of the Ozarks. The occurrence of such United States species in Guatemala as *Panicum villosissimum, Myrica cerifera, Scleria oligantha, Carpinus caroliniana* var. *tropicalis, Ostrya virginiana* var. *guatemalensis, Liquidambar styraciflua, Rhus radicans, Cyrilla racemiflora, Acer negundo, Berchemia scandens, Parthenocissus quinquefolia, Ascyrum hypericoides, Proserpinaca palustris, Berula erecta, Chimaphila umbellata, Monotropa hypopitys, Gelsemium sempervirens, Cephalanthus occidentalis, Mitchella repens,* and *Chrysopsis graminifolia,* of which a large number are species now found on the youthful Coastal Plain area of the South Atlantic and Gulf States, shows that they are definitely more related to the flora of the eastern than to that of western United States. A number of the species just mentioned are known in Guatemala to occur only on the ancient core of Paleozoic and Mesozoic strata, and probably represent some of the oldest elements of the Guatemalan flora. In these cases it is believed that during the early part of the Tertiary period following widespread submergence by Cretaceous seas in Guatemala and the west-central part of the United States, the area of the eastern United States (especially the Appalachian and Ozark regions), most of Mexico, and part of Central America (including Guatemala) was opened to continuous plant migration. Invasion and interchange of the floras took place over this wide area while the land was reduced to a low-lying peneplain. But following later Tertiary uplifts, many of the land connections were disrupted and much of the flora failed to survive. Thus, the occurrence of *Liquidambar, Rhus radicans, Berchemia, Parthenocissus, Ascyrum, Gelsemium,* and *Mitchella,* confined at present in Guatemala to remote, elevated, mountainous and stratigraphically ancient parts where they are separated by hundreds or thousands of miles from their nearest known stations in Mexico or the United States, would indicate that these are relic species of former more widespread distribution. Since these species are also Coastal Plain types that apparently manifest a relationship with a previously existing Appalachian Upland ancestry, it is probable that they represent examples of distribution of ancient and apparently early Tertiary types. This Coastal Plain area was not available to occupation by the flora until Quaternary and Recent times. Therefore, the flora of the Appalachian and Mexican plateaus, and of parts of Guatemala now occupied by this flora, must have occupied a land surface available for plant occupation before the later migration to the younger Coastal Plain occurred.

The second part of the relationship, namely, that of species related to the flora of the Rocky Mountains, consists of a noteworthy group confined in Guatemala to the cooler regions. Some of the characteristic genera are *Abies, Cupressus, Juniperus, Calochortus, Zigadenus, Montia, Erysimum, Amelanchier, Eysenhardtia, Eucnide, Gaura, Arbutus, Penstemon, Houstonia, Symphoricarpos, Selloa, Pina-*

ropappus, and *Carminatia.* The Guatemalan species of these genera are closely related to North American species, but have become differentiated into distinct types either indigenous to Guatemala or found only in Mexico and Guatemala or adjacent Honduras and Salvador. Many of these genera reach their southern limits of distribution in Guatemala, and have their center of distribution in Mexico, or are definitely related to species of the Rocky Mountains or of the southwestern United States.

This two-fold relationship with the flora of the United States, one of species whose main distribution is with that of the southeastern United States, and the other with that of the western and southwestern United States, would indicate the following: that the Cretaceous seas which invaded the west-central United States so divided the flora of the eastern and western United States that the corresponding components of those floras reached Guatemala at various times following the withdrawal of those seas. The element of the flora of the eastern portion of the United States that reached Guatemala may have invaded that country at the end of the Cretaceous or early Tertiary when both regions were low-lying and peneplained, and previous to the later uplifts. The floral element from the western portion of the United States that reached Guatemala and other parts of Central America may have invaded at a similar time or as late as the Pliocene, either preceding or coincident with the last Pliocene uplift of Guatemala.

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DIFFERENCES IN TOLERATION OF DRYING BETWEEN SPECIES OF TERMITES (RETICULITERMES)

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INTRODUCTION

Species differences in toleration of extreme variations of certain ecologically important factors provide indications of the action of natural selection in species divergence. Cases in which differential tolerance of environmental variations can be correlated with distribution patterns are of particular interest to students of ecology and evolution.

Three species of termites in the Chicago area have been studied to determine differential resistance to drying, and the possible correlation with distribution patterns.

MATERIAL

The termite fauna of the Chicago area includes a typically western desert and prairie form, *Reticulitermes tibialis* Banks; an eastern termite found in mesophytic forests, *R. flavipes* (Kollar); and a termite that appears to be confined to sand dunes in the Chicago area, but with less well known habitat relations, *R. arenincola* Goellner.

The most serious difficulty in making such studies on termites is the gradual metamorphosis characteristic of the order. In selecting individual workers, soldiers, and reproductives for use in an experiment, it was impossible to obtain animals of the same age, or to know the ages of the individuals selected. For this reason, animals were used in large groups containing representatives of the three castes. Fifty was chosen for the group size, and an attempt was made to approximate the apparent caste proportions of the colonies under natural conditions. The experimental group was made up of forty-six workers, two soldiers, and two reproductives. The following criteria were adopted in selecting individuals for experimentation: workers, maximum size with full pigmentation; soldiers, maximum size with full pigmentation of head and mandibles; reproductives, nymphs with well developed wing pads, if available, and if not, the largest secondary reproductives in the colony.

Toleration experiments on insects with complete metamorphosis or with clearly defined nymphal instars can be conducted using smaller numbers. With termites, it was thought that the use of large numbers would help reduce errors due to age differences in the individuals tested.

Another difficulty arose from the fact that two of the species studied came from the Indiana dunes where wide extremes of temperature and humidity were frequent, while the third species, *R. flavipes*, was collected from the back yard of Whitman Laboratory of the University of Chicago, in the metropolitan district, a cool moist environment in summer, and one probably close to the optimum for that species. Results of preliminary experiments indicated that natural environmental conditions were a factor in determining the survival time of the group when exposed to dry air. An attempt was made, therefore, to equalize the pre-experimental environment for animals to be tested by exposing them to nearly optimal conditions for known lengths of time before determining the resistance to drying.

Early in the course of the investigations, pieces of wood containing the termite colonies were collected in the field and brought back to the laboratory intact, wrapped in newspaper. Then the pieces of wood were carefully broken and the termites removed and placed in clean glass bowls. They remained in the bowls

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just long enough to enable the investigator to obtain fifty experimental animals each of two different species with the desired caste proportions. Termites compared in this manner will be referred to in the tables and graphs as "From Field."

Later in the course of the investigations, the termites were collected as before, but were placed in groups of 500 in finger-bowls containing a moisture-retaining layer of a mixture of agar and sawdust which served as food. Animals maintained on this medium for a period of two or more days before being used in an experiment will be referred to in the tables and graphs as "Agar."

Other groups of termites were cultured in finger-bowls containing the agar-sawdust medium with a layer one-half inch deep of sand and nest fragments on top of the agar. Animals so treated will be referred to as "Agar-Sand." Termites were also cultured on the agar-sawdust medium inside the incubator at 34° C. for two or more days. These will be referred to as "Agar-Incubator."

Experimental Apparatus

The apparatus used in obtaining air of desired dryness consisted of compressed air, from a wall source, which was bubbled through a wash-bottle of water; a large condensation jar kept under a stream of cold water; three smaller condensation jars, kept in a bowl of ice; three aspirator jars of one liter capacity containing anhydrous calcium sulphate; two aspirator jars of the same size containing anhydrous calcium sulphate impregnated with cobalt chloride; a hygrometer jar, a battery jar with a paraffin-impregnated cork with two glass tubes inserted in it; a "t" connection leading to the two specimen tubes; the specimen tubes; and an outlet tube.

The air flowed through the wash-bottle, losing what grease or dust it may have carried, and then, by means of rubber tubing, was led through the condensation jars, where some of the moisture was taken from it. This part of the apparatus was kept in a sink and on a water table immediately behind it. The air was then led to an incubator, which was placed on a table near the sink. Air entered the incubator through a hole near the top, in which a two-hole rubber stopper was inserted. Glass tubes were placed in the stopper, and by appropriate connections on the inside of the incubator, served for inlet and outlet tubes. The drying jars and the rest of the apparatus were kept inside the incubator, which had two shelves in addition to floor space.

The drying jars were connected so that air entered at the bottom of the jar and flowed up through the desiccating agent, out the top, and then to the bottom of the next jar.

Air entering the hygrometer jar flowed directly through an opening in the hygrometer housing, so that a maximum exposure of the sensitive element was obtained. This was accomplished by bending the glass inlet tube, making a flared lip, and pushing it down through the stopper to a point beside the opening in the hygrometer housing.

The air velocity used was sufficient to displace 2,260 cc. of water in eighteen seconds, or 7,530 cc. per minute. The velocity was determined before and after the experiments by timing the displacement of water from a jar which, when filled to the top, contained 2,260 cc. of water.

The desiccating agent

Anhydrous calcium sulphate or "Drierite" (Hammond Drierite Co., '48) was employed with satisfactory results for drying the air. It was convenient to use both the plain type and the indicating type (calcium sulphate impregnated with cobalt chloride). The indicating type is bright blue when anhydrous, and turns rose red after absorption of water. Jars of the indicating compound in the experimental apparatus showed when the plain desiccant needed change and regeneration. About twelve pounds of the drying agent, of 8-mesh granule size, dried air to a humidity of two per cent for about twenty

hours, at the velocity employed. As a matter of precaution, however, the first jar of the desiccant to receive air from the condensation jars was changed at the beginning of each experiment.

Regeneration of the calcium sulphate was accomplished by heating the material in an ordinary gas oven at 450° F. for two hours. The desiccant was spread in a layer about one inch thick on a metal tray and heated. It was placed in storage jars while hot and covered tightly until used.

Anhydrous calcium sulphate was chosen for the experiments because of its high drying efficiency, inertness toward the constituents of air exclusive of water vapor, lack of toxicity, and the ease with which it could be handled.

The hygrometer

A Laboratory Standard Hygrometer, Type HGS-HY-1, No. 485, made by Serdex, Inc., was used to measure the relative humidity. This instrument was designed to measure the ambient value of relative humidity, and gave direct readings in per cent relative humidity. The accuracy was ± 1.5% between 15% and 100%. It is probable that the accuracy was somewhat less at the 0–2% relative humidity employed in the experiments, but there was no way to calibrate it at that extreme degree of dryness. The sensitivity depends upon the ventilation rate, and at the air velocity employed in this work, it required about five minutes to move from the points indicating the room humidity (50–70%) to the 0–2% point used in the experiments.

The specimen tubes

The specimen tubes consisted of two glass tubes 19 cm. long, with an inside diameter of 2.2 cm., having corks at both ends, leaving about 16 cm. free space for the termites. The corks were bored and a wide glass tube inserted in each cork. The surface of the cork on the inside of the tube was coated with a layer of paraffin to delay attack by the termites. The inner ends of the tubes in the corks were covered with gauze bandage cut in small circles. The gauze was held in place on the inside of the tube by a circle of brass "turnings." Air flowed through the gauze readily, and this arrangement kept the animals within view of the observer at all times.

Air came to the specimen tubes after going through the hygrometer jar. Rubber tubing connected the outlet of the hygrometer jar to a glass "t" connection, and from there the air flowed through the two glass tubes inserted in the corks of the specimen tubes. There was a similar "t" connection at the opposite ends of the specimen tubes, and from there the air went to the outlet tube.

The specimen tubes were washed and wiped between experiments to remove sand grains, faecal material, and fingerprints from handling, so that a maximum of visibility was obtained. The tubes were suspended one above the other in a wooden rack, with a thermometer between them.

The incubator

The incubator used varied about 1° C., and was equipped with a circulating mechanism to insure even temperature throughout. 34° C. was the temperature used for the experiments and also for growing the termites.

The Experiments

The experiments were run in pairs. Fifty individuals of each species, in groups of forty-six workers, two soldiers, and two reproductives, were used in each experiment, with the exception of a few experiments designed to test caste differences within a colony. Records were kept of the caste of the individual when its end point had been reached. It was impossible to determine accurately when death occurred, so an end point was chosen.

Termites died under the experimental conditions in a fairly consistent manner; they fell on their backs and moved all six legs rapidly and in a coordinated manner

for a time, then got up and walked about again, then fell, got up, and repeated this for some time, but the period between falling down and getting up became progressively greater, until eventually they fell and remained down. The end point was taken as the point at which the animal had fallen and remained down; when the legs were held closely to the body and presented a rigid appearance; when the antennae had become bent in a semi-circle, pointing backward; and when the legs moved so slowly that the animal would be unable to rise again, as shown by previous experience.

There were a few cases of termites not conforming to this general picture, and if an individual got up and walked after it was thought to have reached the end point, a correction was made on the data sheet.

Observations were begun 120 minutes after the start of an experiment, and taken every 30 minutes thereafter. In taking observations, the outer door of the incubator was opened and readings taken through the glass inner door without opening it. Variations in temperature during observations were not sufficient to register on the thermometer.

Method of handling

The animals were transferred from the colonies in wood to the bowls and specimen tubes by a method that resulted in no visible injury. The termites were picked up easily and quickly on paper spatulas, made from heavy bond paper folded to form a stiff handle and the folds cut back at one end to leave a blade of one thickness. Gently inserting the blade

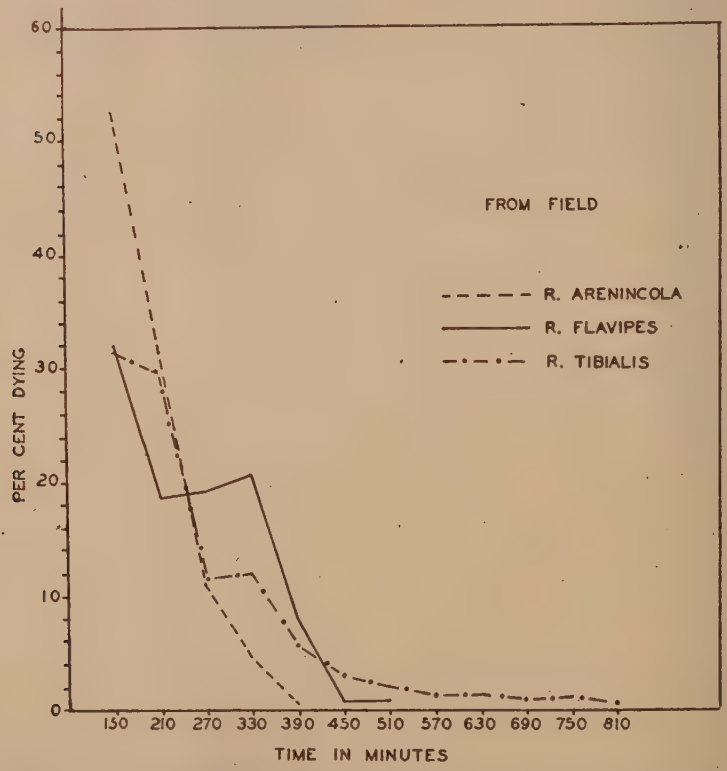

FIG. 1. Percentages of individuals dying during 1-hour intervals. For numbers of individuals, see table I.

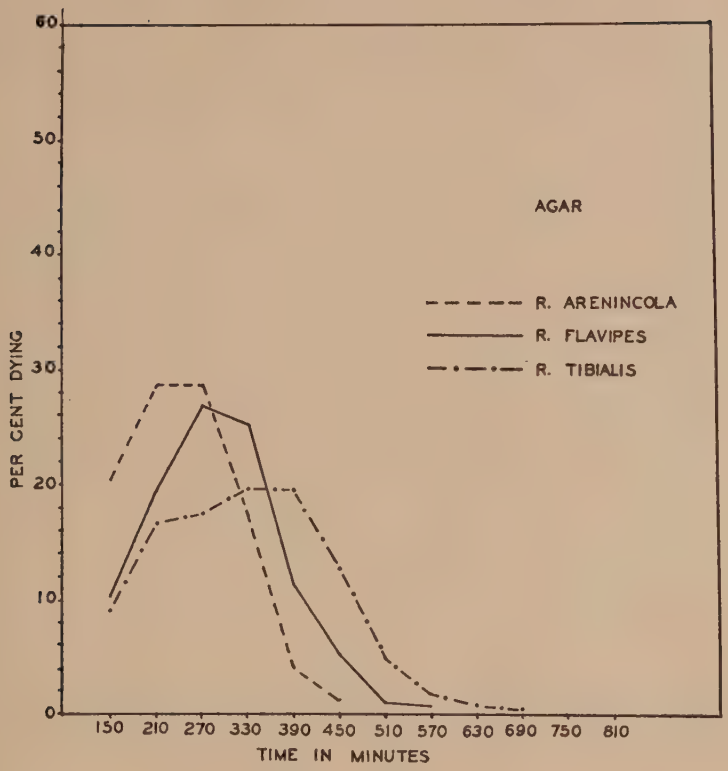

FIG. 2. Percentages of individuals dying during 1-hour intervals. Termites tested after culturing two days on agar-sawdust medium. See table I for numbers of individuals.

beneath the legs of the termites usually resulted in their crawling up on it, particularly if a dead individual had been crushed and rubbed on the blade. The termites clung to the paper while being moved from one bowl to the other, and a gentle tap on the handle was usually sufficient to dislodge them. They were picked up from glass dishes more readily than from wood, paper, or the medium in the culture dishes.

In conducting experiments on termites from the agar or agar-sand culture dishes, a large number were dislodged by inverting and gently tapping the dish over a clean finger-bowl. Fifty of them were transferred to one of the specimen tubes and a similar group of fifty left in a finger-bowl to be used in the incubator as a control.

Controls

Three types of controls had to be employed to establish the fact that deaths in the experimental animals resulted from drying.

(1) To exclude the possibility that air flow was injuring the termites, several experiments were run with the air flowing at the experimental velocity through the wash-bottle but not the jars of the desiccant, so that the air had a relative humidity above 95%. These experiments had to be terminated at the end of twenty-four hours, as the animals did not die and even began excavations in the paraffin-covered corks in the ends of the specimen tubes.

(2) To exclude the possibility of death resulting from temperature acting alone,

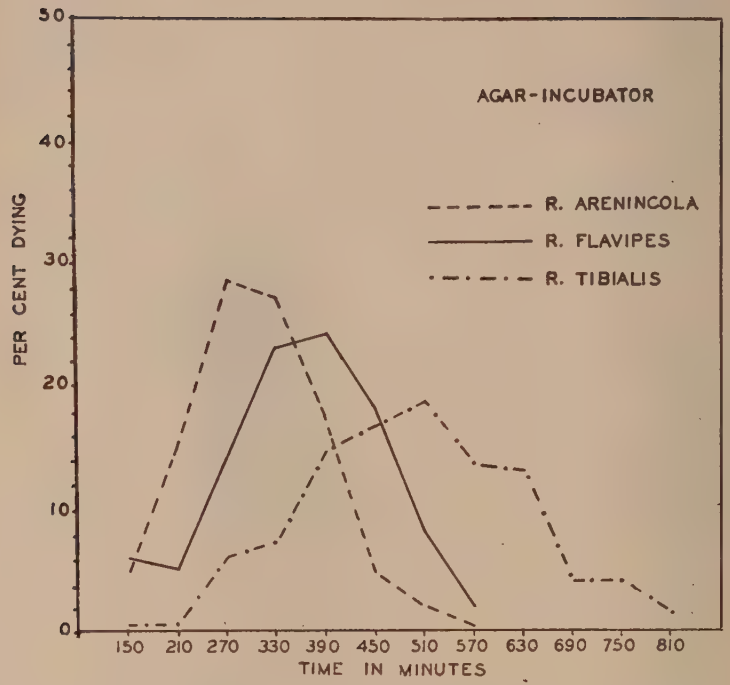

FIG. 3. Percentages of individuals dying during 1-hour intervals, tested after culturing two days on the agar-sawdust medium in the incubator at 34° C.

the preceding test was used. Also, the animals were cultured at 34° C. for periods up to two months.

(3) To exclude the possibility of death resulting from injuries in removal from the galleries, bowls containing groups similar in number and caste composition to the experimental groups were placed in the incubator, with wet paper towel and covered to prevent evaporation. No deaths occurred in these groups during the period of an experiment. There was a careful selection of individuals for experimental animals and for controls, and no termite showing injury was used. However, injuries not apparent to the

TABLE I. *Results of experiments testing species differences in survival time under conditions of extreme dryness*

Culture method	Species	Number tested	Average survival time in minutes ± s.e.*	σ
From field	*R. arenincola*	200	174 ±3.8	54.21
	R. flavipes	400	230 ±4.5	89.61
	R. tibialis	500	234 ±5.6	126.00
Agar	*R. arenincola*	700	229 ±2.6	68.80
	R. flavipes	700	274 ±3.2	85.47
	R. tibialis	1,050	310 ±3.2	106.60
Agar-incubator	*R. arenincola*	250	292 ±5.1	80.11
	R. flavipes	100	345 ±9.6	96.14
	R. tibialis	200	482 ±9.1	129.70

* = Standard error
σ = Standard deviation

TABLE II. *Statistical comparisons between the species listed in table I.*

Culture method	Species comparisons	Probability
From field	*R. arenincola/R. flavipes*	<0.001
	R. arenincola/R. tibialis	<0.001
	R. flavipes/R. tibialis	<0.60
		>0.50
Agar	*R. arenincola/R. flavipes*	<0.001
	R. arenincola/R. tibialis	<0.001
	R. flavipes/R. tibialis	<0.001
Agar-incubator	*R. arenincola/R. flavipes*	<0.001
	R. arenincola/R. tibialis	<0.001
	R. flavipes/R. tibialis	<0.001

observer and not sufficient to cause death under otherwise favorable circumstances may have contributed to the high early mortality in the "From Field" experiments.

Results

The results of the experiments are summarized in tables I and II. Graphic representation will be found in figures 1, 2, and 3.

Wide differences in survival time were observed between termites cultured on the agar-sawdust medium and those cultured on the agar-sawdust medium with sand and nest fragments. To exclude the possibility that these differences were a result of accidents of sampling, some experiments were conducted in which colonies were divided into halves and cultured on the two types of media. Then average survival time for the groups was determined. The data obtained are shown in table III, and are represented graphically in figures 4, 5, and 6. It will be noted that there are slight differences between the means of groups cultured on the agar-sawdust medium in these experiments and the means given in table I. This is a result of the smaller number of individuals involved. The means of these experiments are well within the range of variation of the means of separate experiments in the other series of tests on termites cultured on the agar-sawdust medium.

The observed differences between termites cultured in the agar-sawdust medium and those cultured on the medium with sand and nest fragments theoreti-

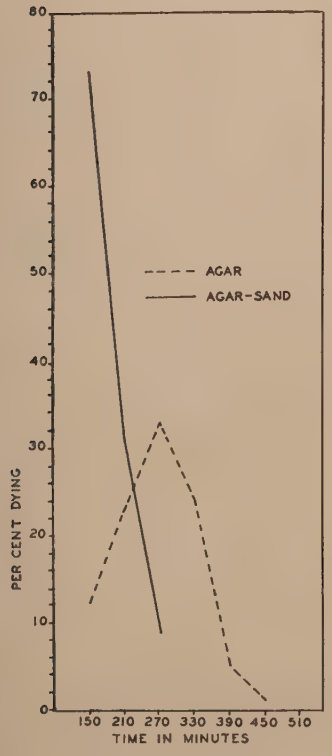

Fig. 4. *R. arenincola*

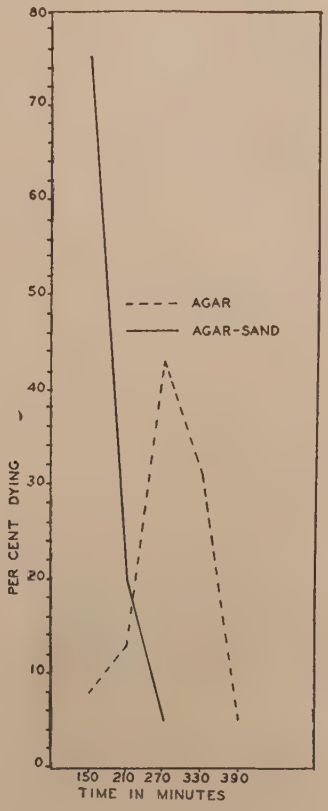

Fig. 5. *R. flavipes*

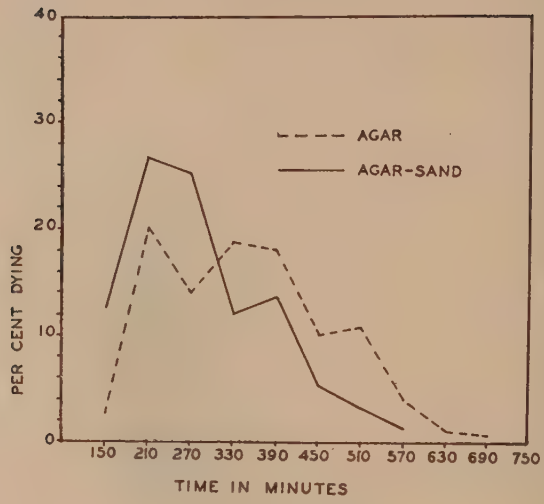

Fig. 6. *R. tibialis*

FIGS. 4–6. Percentages of termites dying during 1-hour intervals, one group tested after culturing two days on the agar-sawdust medium, the other tested after culture on the agar-sawdust medium with sand and nest fragments. See table III for further details.

cally might have resulted from differential abrasion of the body surface that affected evaporation. To test this postulate, termites were removed from a culture bowl of the agar-sawdust medium and subjected to sand particles blown against them and vigorous agitation in a bowl of dry sand. Resistance to drying of these "sand blasted" termites was then compared to that of untreated members of the same colony. The results of these experiments are given in table IV.

No significant differences in survival time were produced by exposing termites to the abrasive action of the sand. Larger numbers should probably have been employed here, but it is evident from comparisons between these experiments and those conducted on termites cultured for some time on the two types of media that some factor other than exposure to sand is operative in producing effects on survival time. This is in contrast to the findings of Wigglesworth ('45), who has shown that abrasions of the cuticle are important in determining resistance to desiccation in the Reduviid bug *Rhodnius prolixus*.

The observation that termites will remain in the sand and nest fragments instead of excavating in the agar-sawdust medium when both are available offers an alternative explanation of the observed differences in survival time between ter-

TABLE III. *Comparisons of survival time of termites cultured on the agar-sawdust medium and the agar-sawdust medium with sand and nest fragments*

Species	Number in agar-sand	Average survival time in minutes ± s.e.	σ	Number in agar	Average survival time in minutes ± s.e.	σ	Probability
R. arenincola	150	150±2.5	38.73	150	243±5.2	64.67	<0.001
R. flavipes	100	148±3.7	37.08	100	263±5.9	58.71	<0.001
R. tibialis	150	269±7.8	95.90	150	337±9.3	115.00	<0.001

TABLE IV. *Resistance to drying of "sand blasted" termites compared to that of untreated members of the same colony*

Species	Number sand blasted	Average survival time in minutes ± s.e.	σ	Number untreated	Average survival time in minutes ± s.e.	σ	Probability
R. arenincola	100	238±6.58	65.84	100	254±7.52	75.24	<0.2 >0.1
R. flavipes	50	194±6.47	45.79	50	196±8.30	58.86	<0.9 >0.8
R. tibialis	100	278±10.32	100.32	100	303±9.56	95.61	<0.1 >0.05

mites cultured on the two types of media. The termites eating through the medium would certainly have a higher moisture content in the gut than those subsisting on the rather dry wood particles of the old nest fragments, and amount of fluid in the body may be an important factor in determining survival time.

Experiments designed to test caste differences in tolerance to drying are of interest in connection with the preceding suggestion concerning the role of fluids in resistance to drying. The results of these experiments are presented in tables V and VI.

TABLE V. *Results of experiments designed to test caste differences within colonies in resistance to drying*

Species	Castes, number	Average survival time in minutes ± s.e.	σ
R. flavipes	1 worker 24 imagoes	69± 3.17	15.87
	2 workers 23 nymphs	150±12.40	61.91
	21 workers 2 soldiers 2 nymphs	78± 9.67	48.37
	25 imagoes	80± 3.47	17.35
R. arenincola	50 soldiers	165± 1.67	12.85
	46 workers 2 soldiers 2 nymphs	229± 7.89	56.52
	3 workers 35 soldiers 2 nymphs	185± 9.5	60.33
	36 workers 2 soldiers 2 nymphs	212± 9.3	59.00

The experiments on *R. flavipes* were performed using an air pump for pulling air through the desiccating agent and the specimen tubes, and it was impossible to measure the velocity. Thus the results of these experiments are not directly comparable with the experiments summarized in table I, in which compressed air at a constant and measurable velocity was employed.

The differences between soldiers and the mixed groups consisting of all three castes have been obtained in duplications of these tests, using a slightly different technique. Differences between nymphs and the other castes, including the imagoes, are striking, and appear in all cases. Differences between soldiers and workers are detectable only when all-soldier groups are compared with mixed groups. Imagoes appear not to differ from the workers and soldiers in resistance to dry-

TABLE VI. *Statistical comparisons between the caste-groups given in table V*

Species	Comparisons	Probability
R. flavipes	imagoes, worker/ nymphs, workers	<0.001
	imagoes/workers, soldiers, nymphs	<0.9 >0.8
R. arenincola	soldiers/workers, soldiers, nymphs	<0.001
	3 workers, 35 soldiers, 2 nymphs/36 workers, 2 soldiers, 2 nymphs	0.05

ing, although the imago has a more rigid and probably thicker exoskeleton. The imagoes are also fully pigmented, and are typical winged insects, in contrast to the wingless, pale, thinly covered workers and soldiers.

Ecological Distribution

A study was undertaken with the aim of determining local distribution patterns of the two dunes species, *R. tibialis* and *R. arenincola*. The associations recognized were the middle beach, cottonwoods, and pines or oaks and pines, as defined by Shelford ('13). These habitats are also described by Talbot ('34).

In this study, the middle beach was taken as a starting point and as large an area as possible was covered paralleling the margin of Lake Michigan. Several soldiers were removed from each colony found, and with a locality and association label, placed in a vial of 85% alcohol. After the middle beach had been covered thoroughly an area of approximately equal extent was covered in the cottonwoods in the same manner. The pine and oak-pine woods could not be treated in this way, owing to extensive housing developments at Miller, Ogden, and Michigan City. Here, colonies were taken as found, irrespective of the area covered, and the larger number of colonies taken is not necessarily an indication of denser populations in this association compared to the others.

The localities visited in the distribution study included Miller, Cavanaugh, Ogden Dunes, Michigan City, and the Indiana Dunes State Park, all in Indiana; and Sawyer, Michigan. *R. tibialis* was collected in each of the above localities; *R. arenincola* was taken at Miller, Michigan City, and the Indiana Dunes State Park.

Although *R. flavipes* was not included in the distribution study, the local distribution is of interest. It has been collected by Dr. Alfred Emerson at Valparaiso, Smith, and Turkey Run, in Indiana; Sawyer, Michigan; and at Chicago and Peoria, in Illinois. All of these localities except Chicago and Peoria are covered with beech-maple climax forests or cleared and cultivated land replacing the climax forest. The vegetation of Chicago and Peoria originally included oak, hickory, basswood, and elm (Shelford, '13).

Identifications of the termites collected were made from the soldier caste alone, as there were no imagoes in the colonies during the period in which the collections were made.

R. arenincola and *R. tibialis* showed the following distribution pattern:

	arenincola	*tibialis*
Middle beach	0	12
Cottonwoods	0	24
Oaks, Oaks-pines	36	50

There is a difference in moisture content of the soil in the three associations, as shown by Fuller's data on wilting coefficients cited by Shelford ('13), with evaporation rate decreasing as one goes from the middle beach through the oak association to the beech-maple climax.

Discussion

It is probable that moisture in food or as free water consumed by termites prior to experimental testing is the most important single factor in resistance to drying as determined in this work. This is indicated by the greatly increased toleration to dry conditions shown by animals cultured on the agar-sawdust medium when compared with animals tested immediately after collecting, particularly in the dunes species. The increased resistance to drying following culture in the incubator may be a result of increased consumption and more rapid digestion of the food medium that had a high water content.

All-soldier groups provide valuable comparative material, since transfer of fluids between individuals is unlikely unless workers are present. That the all-soldier groups are less resistant to drying than worker-soldier groups is important evidence of the role of fluids and transfer

of fluids in determining group survival time.

The greatest difficulty with this suggestion is that *R. flavipes,* the largest of the three species (and probably the one with the greatest fluid content), is less tolerant to dryness than *R. tibialis,* the termite intermediate in size between the other two species.

The fact that toleration of dryness was not correlated with size indicates that differences in surface-volume ratios are not the only factors in species differences in survival time under the experimental conditions. This suggests further that evaporation from the general body surface is not as important here as Wigglesworth ('45) found it to be in the Reduviid bug, *Rhodnius.*

The rather unexpected similarity in tolerance of dryness shown by imagoes and the non-sexual castes within a single species indicates that the observed cuticular differences may not be primary in determining survival time in termites. The much greater resistance shown by nymphs just prior to the last molt, and by supplementary reproductives, further suggests the importance of fluid content in determining survival time. The reproductive nymphs and supplementary reproductives are much larger forms than the imagoes of the same species, and seem to be distended with fluids.

With these facts in mind, it was necessary to expose the experimental animals to controlled conditions, as already described, before attempting to establish species differences.

An increase in resistance to drying followed culture on the agar-sawdust medium in all three species, but the increase was most pronounced in *R. tibialis,* next in *R. arenincola,* and least in *R. flavipes.* This is in keeping with the observation that conditions were most nearly optimal in the environment from which the *flavipes* colonies were taken. In the "From Field" experiments, *R. tibialis* and *R. arenincola* did not give consistent and repeatable results when tested, no doubt because of the variable degree of dryness in the environments from which they were collected. *R. flavipes,* on the other hand, coming from optimal, or nearly optimal conditions, did not show so pronounced an increase in resistance to drying after laboratory culture, and showed a sharp decrease after culture on the agar-sawdust medium with sand and nest fragments.

The observed differences in tolerance to dryness in the species of *Reticulitermes* in the Chicago area seem to be correlated with their local and general distribution. *R. tibialis* is characteristically an inhabitant of arid areas in prairies and deserts from Indiana to Lower California, although it is not wholly confined to extreme desert conditions. *R. flavipes* is a termite of the eastern mesophytic forests ranging from Florida to Maine and west to the prairie borders.

R. arenincola, the species that showed the lowest survival time under the experimental conditions, is ordinarily regarded as a dunes form in the Chicago area. It would be more nearly correct to regard it as an inhabitant of mesophytic forests on sand in some parts of the Chicago area. That it is less resistant to drying than *R. flavipes,* an inhabitant of the very moist beech-maple climax forests, is an interesting inconsistency in the broad picture of ecological distribution correlated with physiological toleration among species of *Reticulitermes.*

The social habits of termites result in a certain control over the nest humidity, particularly among the more highly evolved genera. Fyfe and Gay ('38) found that *Nasutitermes exitiosus* (Hill), a mound building termite in Australia, regulated nest humidity very precisely, and kept it at a high level. This is accomplished by preventing evaporation of soil water and metabolic water, which appears to be effected by differential construction of the nest walls. In the mound nests of this species, the inner walls are thinner and contain a higher percentage of organic matter than the outer walls. The inner walls have some undetermined

properties that prevent the deposition of free water on them, in spite of the high humidity inside the mound (Holdaway, '33).

The social homeostatic control over humidity fluctuations obtained by nest construction appears to be less perfect in the relatively more primitive genus *Reticulitermes*. In areas of extreme dryness, as in the Indiana dunes, one may frequently find very dry but apparently flourishing colonies of *R. tibialis*. Population size may be a factor in survival, as a large colony may have sufficient fluid reserve to survive until the next rain. However, reproductive pairs after a colonizing flight face environmental exigencies more directly than the established colonies, without the large fluid reserve. Flights usually occur after a rain, but the beginning stages of colony development are subject to variations in availability of water for a considerable time, unless the reproductive pair excavates in a spot with easily available moisture at not too great a depth. Such conditions would prevail in the oak association in the spring, but, in the cottonwoods and on the middle beach, the sand may become dry for several inches, except in rainy weather. It is probable that selection, with dryness as the selective agent, is most effective in the early stages of colony formation. This could be the explanation for the apparent failure of *R. arenincola* to invade the cottonwood and middle beach associations in the Chicago area. That it is not a competitive biotic factor preventing spread is suggested by the presence of *R. tibialis* and *R. arenincola* together in the oak association.

Efforts to collect *R. flavipes* in the mesophytic forest association on sand at Sawyer, Michigan, were unsuccessful, but the species has been taken there by Emerson and Goellner. The distribution pattern here appears to be quite diagrammatic, with *R. tibialis* on the beach and ranging back through the oaks, and *R. flavipes* inhabiting the beech-maple climax immediately adjacent to the oaks. There are only a few collection records for this area, however.

All three of the species of *Reticulitermes* under consideration have invaded the Chicago area since the retreat of the last glacier, but by different routes. *R. tibialis* probably came in from the west, *R. flavipes* from the east, and *R. arenincola* from the south. *R. arenincola* shows close morphological relationship to *R. virginicus* Banks, a southern representative of the genus, and probably diverged from it, later invading more northern areas. The distribution records are meager, however, and this must remain conjecture until further data are obtained.

Species differences in resistance to drying correlated with ecological distribution have been demonstrated in certain ants of the genus *Formica* by Talbot ('34). She found that different species replaced each other in different stages of the dunes succession in the Chicago area, and that physiological toleration was correlated with the particular association inhabited by the species.

Comparisons between *R. tibialis* and *R. hesperus* Banks, a far western termite, with respect to their soil-moisture requirements have been made by Williams ('34). In California, *R. tibialis* was found in drier areas than was *R. hesperus* and, according to his experimental findings, *tibialis* colonies were able to excavate and survive in soil with a lower moisture content than that necessary for *R. hesperus*. He further found that *R. hesperus* was better able to survive in high carbon dioxide concentrations than *R. tibialis*. These two factors are probably of great importance in survival in a given habitat of the two species. He concluded that the differences, though slight, were probably sufficient to be of importance in the distribution of the two species.

The differences between species observed in the course of this investigation have also been relatively small, but it is at least theoretically possible that the difference in tolerance to dryness is great enough to prevent the expansion of *R.*

arenincola into the cottonwoods and middle beach associations, while *R. tibialis* can exist in both in fair abundance. This may or may not be the factor limiting *R. flavipes* to mesophytic forests. It is obvious that many factors influence the distribution patterns of these species of termites.

Acknowledgments

The author wishes to acknowledge the valuable guidance of Alfred Emerson, who suggested the problem. The author wishes to thank W. C. Allee for providing space and materials at Whitman Laboratory, Sewall Wright for the use of an incubator, and Harold Finley for the hygrometer and much of the materials used in the experimental apparatus. Thanks are also extended to several colleagues who generously gave their time and facilities for field collecting.

Summary

Three species of the termite genus *Reticulitermes* have been compared in their resistance to drying. It was found that *R. tibialis* showed the greatest resistance, *R. flavipes* was intermediate and *R. arenincola* showed the least resistance to drying. This resistance was measured in average survival time of groups of fifty termites including the three castes.

Tolerance to drying was found to be strongly influenced by the type of environment to which insects of the same species were exposed prior to being tested. The environment is believed to exert this influence through affecting the amount of fluid present in the body, especially in the gut.

Differences in resistance to drying were observed in different castes within a colony, reproductive nymphs and supplementary reproductives showing the greatest resistance, and imagoes, soldiers and workers being about equal, except in the case of all-soldier groups. The lack of correlation between survival time and observable cuticular differences suggests that fluid content may be a more important factor in determining survival time.

Species differences in tolerance of dryness were found to be correlated with the local and general distribution patterns for *R. tibialis* and *R. flavipes*. The ecological relations of *R. arenincola* are still obscure, however.

Survival time was not correlated with size, nor, presumably, with surface-volume ratios, as *R. flavipes*, the largest species, was less resistant than *R. tibialis*. This fact constitutes a difficulty in the postulate that fluid content was most important in determining the survival time, because *R. flavipes* probably has the greatest fluid content.

It was suggested that environmental selection, with dryness as the selective agent, operates most effectively on the mated pairs after the colonizing flight in the interval between leaving the parent colony and the construction of adequate protection against evaporation by their progeny.

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THE DISAPPEARING SLEEPING BEAR DUNE[1]

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Recent changes in the outline and contour of Sleeping Bear dune are so impressive that this paper calls attention to this destruction. Pathways on the windward side of the dune were the beginning of such destruction.

Sleeping Bear dune (fig. 1) is situated at the west end of Leelanau County, Michigan, about 25 miles west of Traverse City and about 4 miles north of Empire. It is perched on a glacial moraine overlooking Lake Michigan on the west. In the region of the Bear the glacial moraine is approximately 300 feet above the surface of Lake Michigan and the dune perched upon its edge is now about 75 feet higher than the moraine surface. This dune was a source of interest long before white men appeared. "It was an ancient landmark when Charlevoix saw it in 1722." (John C. Wright in "The Crooked Tree.") Even now it is of great interest, but too much so for its continued existence.

The Indian legend of the origin of Muckwah ne bod, the Sleeping Bear dune, is as follows: Long ago a mother bear and her two cubs fleeing from forest fires in Wisconsin swam across the big lake to the Michigan side. The mother reached shore first and dragged herself up the steep slope and lay down to await the cubs. But the cubs, worn out by the long swim, sank with the shore in sight. The mother bear lay there grieving, watching the spot where her cubs had drowned. In mercy, the Great Spirit turned the cubs into islands—the present day North and South Manitou Islands—and covered the mother bear with sand—the present Sleeping Bear dune.

Through Indian times and the early white occupancy of the region up to very recently, the appearance of a sleeping bear lying on her side was very obvious to one from a boat on the lake. At the present through excessive erosion the appearance of a sleeping bear is becoming less obvious. As first seen by white people from the lake, a densely vegetated dune approximately 600 × 450 ft and more than 135 ft high was perched at the edge of a plateau 350 ft above the lake.

My own earliest recollection, as seen from a lake steamer about 1896, is that of a 2-humped pile of material, completely covered throughout with dark green vegetation, with a tree or snag projecting above. It was very conspicuous on the skyline. Since that time the snag has disappeared, and much erosion has undercut trees on the windward side, many of which have rolled even down to Lake Michigan itself. Great white sandy patches have replaced the dense green of the earlier dune.

The general region in which the Sleeping Bear dune occurs has been written up in considerable detail by Waterman ('26). An earlier briefer account was written by Fuller ('18), and more recently and more geologically by Dow ('37). However, the photographic illustrations in the 1926 and 1937 papers are not dated.

All investigators agree that the dune is of composite origin; that is, from eroded sandy material of glacial origin and from lake sand blown up the steep bluff; and that vegetation of one kind or another has had a part in the development. Suffice to say, evidence now shows that the dune was more extensive and that formerly its axis was approximately parallel with the shore line of Lake Michigan.

Sleeping Bear dune has repeatedly served as one of the points used in making lake surveys. Perhaps the first path up from the lake made possible the beginning

[1] Contribution No. 504, Department of Botany, Kansas State College, Manhattan, Kansas, and a contribution from the Biological Station of the University of Michigan.

of wind erosion which has caused such a marked change in the dune in recent years. This has changed the axis of the dune from parallel with the shore to right angles with the southwest winds, which have been responsible for the tremendous erosion in modern times. Waterman ('26: 363) says:

"Evidence of this (greater wind erosion) is found in the position of an old surveyor's monument on the top of the dunes. When first seen by the writer in 1915, this post was twenty feet back in the bushes at the top of the dune. The conditions were about the same in 1920 and the width of the belt of shrubs between the open sand and the monument had not greatly decreased in 1923. But in 1925 the edge of the sand slope was at the foot of the post and the rapidity of the recession was evidenced by the number of dead bushes still standing in the sand and slightly in front of the post on either side. This recession has not yet reached the crest of the dune, but if the present rate is continued, the height of the dune will soon begin to decrease." This post was no longer there when the present author was on the dune in 1928.

The effect of this wind erosion of the dune at the southwest—so greatly in excess of any erosion of the bluff and thus the foot of the dune—was to move the southwest "corner" of the dune back from the bluff and so change the axis of the dune.

Observations in 1928

In 1928, when the author first took his ecology class there from the University of Michigan Biological Station, the general picture of the dune was as follows: The northwest quadrant was heavily vegetated with a mesophytic forest of both conifers and hardwoods, including *Thuja occidentalis, Acer saccharum, Tsuga canadensis* and *Sorbus* sp. Many of the trees were nearly 60 cm in diameter. The vegetation reached to the bluff overlooking Lake Michigan. The northeast quadrant (fig. 2) was less heavily vegetated and the sand much looser. There were more shrubs, as *Cornus stolonifera* and *Rhus radicans,* lianas, as *Celastrus scandens* and *Vitis vulpina,* small trees of *Betula papyrifera* and some gnarled *Populus deltoides* at the base. Only a few areas of open sand were visible from a distance. A trail wound around through the bushes in decidedly loose sand. In the high saddle between the "haunches" there was open sand at the base of Thuja snags on the southwest side of what was developing into a windsweep, but mostly the area was covered with thickets of *Cornus stolonifera* and stunted treelets of *Betula papyrifera,* around and between which sand was slowly accumulating. It was through this soft sand that the trail to the top of the Bear wound.

The upper part of the southeast quadrant (fig. 3) was heavily vegetated with coniferous and hardwood trees (Thuja, Abies, Tilia) entangled with shrubs of Cornus, *Prunus virginiana,* and lianas. Patches of *Smilacina stellata* were conspicuous. Plenty of *Rhus radicans* was present. At the south, blowing had felled the trees and on the accumulating sand eastward grasses, *Ammophila breviligulata* and *Calamovilfa longifolia,* were established. Towards the crest bushes of Cornus entwined with Vitis and Celastrus, and stunted Thujas covered the ground to just beyond the crest. They maintained a steep bluff down from which to the southwest was a steep slope on which tree trunks were strewn. A few snags projected above the crest. The southwest quadrant (fig. 3) was sparingly strewn with trunks of trees, sandblasted and bleached. The sand in the steep bluff face at the top of the dune appeared to be of land origin rather than waterwashed lake sand. Conspicuous sloping soil lines of black dense humus were higher than midway up. They were often accompanied by large quantities of land shells and here and there bones of small mammals and birds and an elk tooth (*Cervus canadensis*) (Gates '39).

A high saddle of looser sand (the neck

of the Bear) with dense Cornus bushes and a few snags and some live Thuja trees connected the two haunches of the Bear. The valleys leading to it were pathways of blowing sand.

Later Observations

Little difference was noted from year to year until after 1932, when in the course of the Coast and Geodetic resurvey of the Great Lakes, a station was estab-

Figs. 1–6.

Fig. 1. Looking south to Sleeping Bear dune perched on the plateau overlooking Lake Michigan. From a commercial postcard, undated but purchased about 1915. Note that the forest extends to the edge of the bluff. Compare with figures 5 and 7, taken from the same general direction, but farther inland on account of erosion and figure 4, taken closer.

Fig. 2. Looking west to Sleeping Bear dune. July 21, 1928. Note the small number and low stature of dunelets to the east and northeast of the Bear. Compare with figures 6 and 8, the latter taken from the same direction, but closer.

Fig. 3. Looking north to Sleeping Bear dune. July 21, 1928. Compare with figures 10 and 12.

Fig. 4. Looking southward to the northwest part of Sleeping Bear dune. July 20, 1935. The severe erosion of the winter previous has eliminated the forest previously in contact with the edge of the bluff.

Fig. 5. Looking south to Sleeping Bear dune. July 24, 1937. Note windsweeps developing near the summit and forming dunelets on the left (northeast). Compare with figure 1.

Fig. 6. Looking a little south of west to Sleeping Bear dune. July 22, 1949. Note the windsweeps near the summit and at the south end of the Bear and the many small dunes in the foreground (northeast of dune).

lished on the highest point of the Bear. To set up this station pipe and planks were dragged up the southwest face by horses, making a regular roadway directly in line with the commonest strong winds that could operate on the dune. This then also became the commoner pathway for visitors climbing the dune, since, although steep, the sand was firmer and the climbing easier than on the path on the east or lee slope. This was the beginning of great activity of wind erosion. It was not long before the effects were very visible. The tall pine tree, which may have been 200 years old, had died. It was soon undercut and fell. Erosion by southwest winds soon resulted in sand being blown away from the top and from the vicinity of the Coast and Geodetic Survey station. The platform built over the end of a long pipe was let down about 3 feet in the first year and close to 5 more feet the second year, allowing 8 feet of the pipe to stick straight up in the air. Presumably people climbing to the top of the dune helped dislodge the pipe and stage for by the third summer all had disappeared. The erosion spread out, particularly southward, undercutting gradually the whole southwest slope, dropping down all of the trees and snags by 1941. Some rolled clear down to Lake Michigan, others were used for camp fires. Meanwhile, sand was blown away from this quadrant, in part directly up and over the dune and in part around the southern edge. This latter tended to give a little crescent shape to the southern part of the dune. When the sand started going over the top after it had undercut and dropped the vegetation there, the whole top began to creep eastward, one, two or three feet or more a year.

At the same time a good deal of sand movement took place in the windsweep between what was considered as the fore and back haunches of the bear, spreading destruction to the woods on the northeastward, covering them with a mass of very loose sand. Considerable etching of dead trees just about the sand level was also much in evidence.

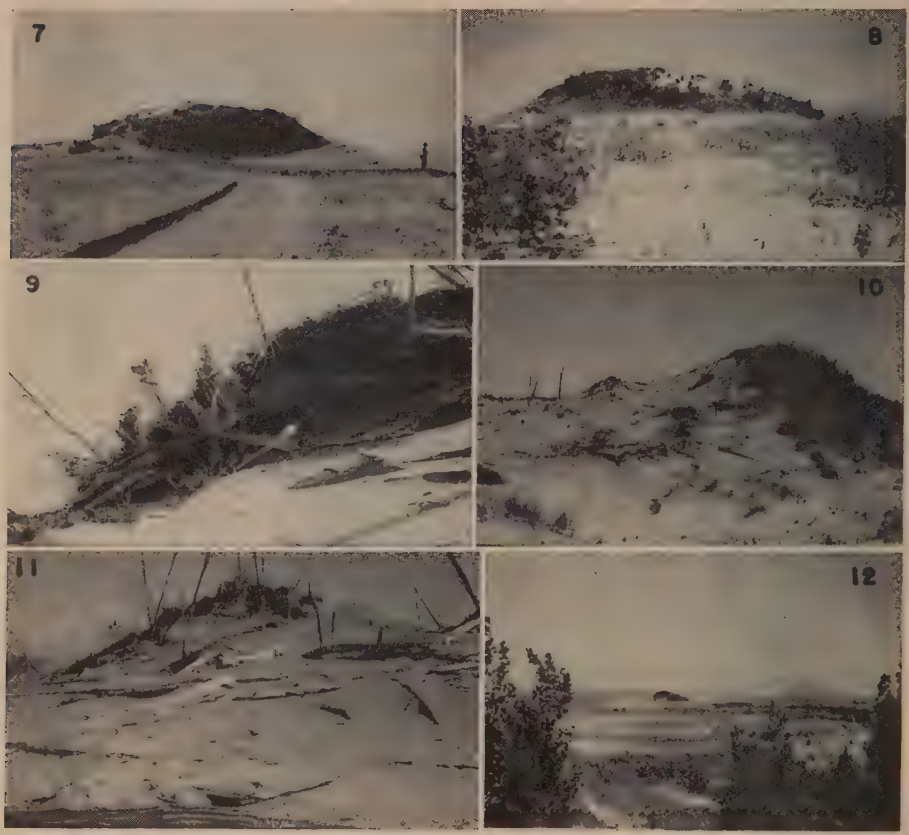
During the 1930's, wind erosion was noticeable but not excessive in the southwest quadrant and in the windsweep in the middle. Commencing in the winter of 1934–35 noticeable changes were beginning in the northwest quadrant (fig. 4). First old trees close to the edge of the bluff began to die and furnish less effective cover to the ground. Blowing began at the bluff edge, the loose sand being carried around the north end out onto the plateau beyond and thence clear away from the Bear.

At the same time erosion was working northward from the middle of the Bear, undercutting the fine hemlock trees, some of which were between 200 and 250 years of age. For a while it was only dead or dying trees that were undercut and felled, but it wasn't long before even healthy living trees were suffering the same fate.

When this erosion had proceeded sufficiently far, the wind, sweeping around the north edge of the dune, cleared the sand completely from the area just above the plateau ridge or edge. This left what appeared to be a 20-foot roadway beginning to climb the northwest side of the Bear, as one saw it from a distance from the north (fig. 5). However it was merely a concentration of pebbles of the plateau remaining after the dune sand had been blown away.

From then on wind erosion has been much augmented. All of the trees in the northwest sector have died. Most have fallen. Many have rolled all or part way down the bluff into Lake Michigan, over 300 feet below. Huge quantities of sand, thus released to blowing, have formed small dunes east of the Bear (fig. 6) or have been swirled away to cross the plateau and be added to the active dunes at the eastern edge of the dune region. This has resulted in a southward retreat of the north edge of the dune 64 meters (210 ft) between 1936 and 1949.

Meanwhile the development of superballoon tires has permitted the establishment of a tourist livery which takes people cruising around in the dunes. For a few years these trips took in only the dunes



FIGS. 7–12.

FIG. 7. Looking southward along the plateau to Sleeping Bear dune. July 24, 1948. Note the auto roadway which swings to the left around to the southwest corner of the dune, also in comparison with figure 5, the more extensive areas of open sand in the northeast quadrant. Compare with figures 1 and 5.

FIG. 8. Looking west to Sleeping Bear dune. July 24, 1948. Note increasing amounts of blown sand in the northeast quadrant. (Photo by Grace Blanchard.) Compare with figure 2.

FIG. 9. A part of the southeast quadrant, showing destruction of the forest. July 22, 1949.

FIG. 10. Looking northeast to destruction in the southwest quadrant. July 24, 1948.

FIG. 11. Looking northeastward to the destruction in the central windsweep (the location of the pathway to the summit in 1932) and in the northwest quadrant. July 22, 1949.

FIG. 12. Looking northward from the "Pinnacle" over the plateau. August 19, 1949. In the center is the Sleeping Bear dune, the west half open sand and the southeast quadrant still with trees. Compare with figure 3, taken much closer.

at Sleeping Bear Point, without being able to get to the Bear itself. About 1946, however, this difficulty was overcome and people are now carried to the very edge of the Bear (fig. 7), and what is worse, to the southwestern corner where the necessity of protection from erosion is greatest. The hazards for the dune are thus greatly increased.

Blowing away of sand, which even in the late 1930's had resulted in complete denudation of vegetation only in the

southwestern quadrant, took on a swifter pace. Sand at the extreme south was carried around the edge of the Bear and deposited to the east in flat plateau-like dunes, most of which became Ammophila or Calamovilfa covered, thus stabilizing somewhat. From the mid part of the southwest quadrant the sand was blown up over the crest of the Bear. For a while bushes of *Cornus stolonifera* and gnarled trees of *Thuja occidentalis* at the top tended to hold the sand, but not for long. They were partly covered within a very few years and died, whereupon some, undercut, fell down the southwest slope—others and the crest itself alike were blown eastward.

In the late 1930's, a new movement of sand up over the bluff from Lake Michigan replaced part of the old dune and in 1940 *Ammophila breviligulata* appeared on it and bid fair to build this new dune up rapidly, but within a couple of years activity had become so great that even the Ammophila itself was blown away as well as all of the sand it had accumulated.

The Bear in 1949

The ground outline of the dune is now nearly elliptical with no vegetation within 50 ft of the bluff.

The east side (fig. 8), as late as 1941 completely covered with vegetation even to hiding almost all of the sand trail to the top, is now more than one-third open loose sand. It still supports a forest (fig. 9) in its southeastern quadrant, but even this forest is being replaced with shrubs and lianas (*Vitis vulpina* and *Celastrus scandens*) and in spots with open sand. Northeastward the loose sand has covered almost all of the vegetation and is on the move at any opportunity away from the Bear out over the plateau.

The west side, towards the lake and the prevailing winds, is now mostly loose sand, sparsely strewn with sand-blasted tree trunks in the southwestern part. In the center is a prominent windsweep which now at times partly covers down tree trunks, now discloses them to sand-blasting. More northward are some living

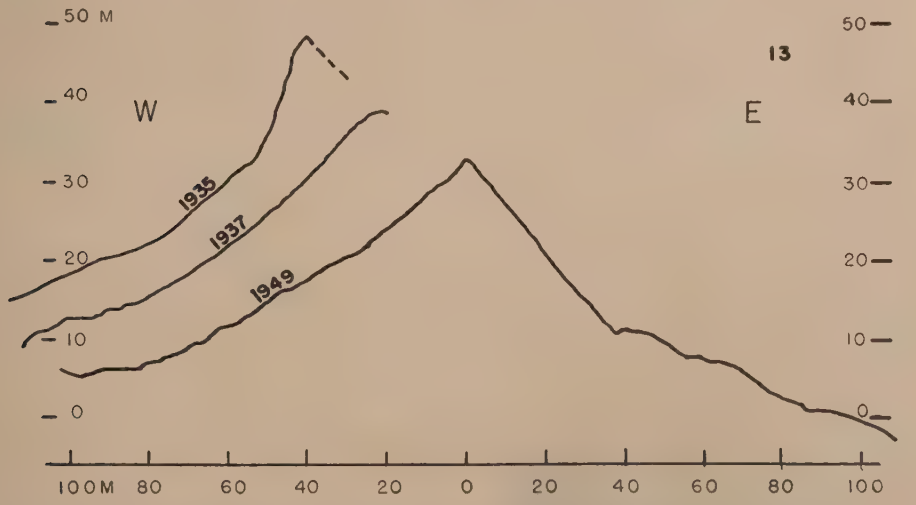


Fig. 13. Showing profiles from the bluff to or through the summit in 1935, 1937, and 1949. The zero of the vertical scale is the elevation of the Coast and Geodetic marker imbedded in a large rock on the plateau north of the dune. It is lower than the elevation of the bluff edge at the dune, but is the only fixed point available. The horizontal scale shows distances in meters east and west from the present center of the dune. The 1949 profile ends at the right at the exposed plateau. The irregularity of the last 65 meters is caused by small dunes made from sand blown from the Bear itself.

woody species mixed in with snags of the former forest, some still standing, many leaning or completely fallen (figs. 10, 11, and 12).

Definite measurements for comparison are difficult because of the lack of base marks on the dune. A Coast and Geodetic monument set in a rock on the plateau, almost north and 1533.9 ft from the survey point on top of the dune, in 1932, gives but direction to the location of the station at that time. Comparing with this arrow, by 1949 the crest of the dune had moved 5° to the eastward. Calculating by trigonometry, the crest has moved eastward about 40.9 m (134 ft) between 1932 and 1949. Heights of the dune were taken from altimeter readings of the monument and of the crest on each of my trips to the area. Early navigation charts credit the top of the dune as being 490 feet above Lake Michigan. This would mean that in the diagram (fig. 13) the top would appear 71.33 meters above the monument and some unknown distance west of the top as given in 1935. In 1935 the top was 48.48 m above the monument. This had decreased to 39.62 m in 1937 and to 33.53 m in 1949. No measurements are available for the recession of the bluff. At the dune it is varying amounts higher than in the vicinity of the monument, which makes the dune lower with reference to the bluff than the heights above the monument indicate. That the bluff itself is receding is obvious from pictures taken northward from the top of the dune, but exact amounts are unknown.

Active blowing has spread to nearly all of the west face of the Bear and sand is being blown—now around the north end, now over the hump, and most frequently around the south end. Blowing has been particularly aggressive in 1948 and 1949. Dunes and dunelets built to the eastward are subtractions from the Bear itself and as replacements up over the bluff from Lake Michigan are inadequate, the Bear can only diminish in size.

Thus it appears that this famous dune, dating ahead of white man's history in the region, by white man's apparently innocent activity is doomed to extinction.

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POPULATION DENSITY AND DISPERSAL RATES IN BRAZILIAN *DROSOPHILA WILLISTONI*

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Introduction

Population density and migration rate under natural conditions are important variables of ecology and of genetics of natural populations. Investigation of these variables has nevertheless progressed little. Experiments were made with some insect species, in which suitably marked specimens were released in their habitats, and then recaptured at various distances from the point of release. Improved techniques of experimentation of this kind and of mathematical treatment of the resulting data have been evolved by Jackson ('40) for tsetse flies, and by Timofeeff-Ressovsky and Timofeeff-Ressovsky ('40) and Dobzhansky and Wright ('43, '47) for species of Drosophila. Individuals marked either by an innocuous mutant trait or by a spot of paint are released at a certain point on the experimental field; at known time intervals after the liberation of marked specimens, collections and records are made of the numbers of marked and of wild individuals found at regularly spaced points at various distances from the point of release. Under favorable conditions, data collected in such experiments permit inference of (1) the type of dispersal characteristic of the released species (for example, Drosophila moves at random in a uniform environment, while tsetse flies tend to establish home ranges), (2) the rate of dispersal under various conditions, (3) the density of the natural population of the species on the experimental field, and (4) the longevity of the released specimens in nature.

Dobzhansky and Wright ('43, '47) found that *Drosophila pseudoobscura* diffuses more or less at random from the point of release, but that the rates of movement are much greater at high than at low temperatures; population densities vary from 0.4 to 10 flies per 100 square meters at the most favorable season of the year on Mount San Jacinto and in the Sierra Nevada, in California; and that under the conditions which prevailed during the experiments, about 10 per cent of the population of released flies died on each successive day.

A study of *Drosophila willistoni,* made with the aid of methods similar to those used previously for *Drosophila pseudoobscura,* is reported in the present article. In *D. willistoni,* we did not possess a mutant which could be identified by inspection with the naked eye in the field. This necessitated examination of the captured flies under a microscope, and made it impossible to release them at the points of the capture and to repeat the process on several successive days. As a result, the type of dispersal and the longevity of *D. willistoni* cannot be ascertained, and in this paper we are forced to assume that in these respects *D. willistoni* and *D. pseudoobscura* are alike. This assumption is almost certainly valid as far as the randomness of dispersal is concerned, but the mortality rates of the two species need not be alike. If the mortality rates differ, our estimates of the population densities of *D. willistoni* and of other Brazilian species are inexact. Since, however, the population densities vary greatly from place to place and from time to time, only the orders of magnitude of the estimates are meaningful.

[1] Contribution No. 4 of the cooperative research project of the University of São Paulo and Columbia University on genetics and ecology of tropical Drosophila.

Experimental Technique

To make the *Drosophila willistoni* flies released on experimental fields distinguishable from wild flies of the same species, we have used the autosomal recessive mutant *hairless* (discovered by Mr. B. Spassky and now re-named *abbreviated*). This mutant differs from wild type by absence of some bristles on the head, thorax, and scutellum. Although *hairless* flies vary with respect to the number and kind of bristles that are missing, and although old wild flies often have some bristles broken, the *hairless* and the normal phenotypes do not overlap and can be, with some practice, distinguished accurately. *Hairless* flies have a good viability, both under laboratory and under natural conditions. Eight young *hairless* flies were found on an experimental field some five weeks after 4,700 *hairless* individuals were released on that field; since *hairless* occurs rarely, if at all, in the wild, the capture of young mutant flies shows that the released *hairless* flies have reproduced, and their offspring have developed and survived, in competition with wild flies.

The experiments were conducted at the Horto Florestal, Cantareira, on the outskirts of São Paulo. Horto Florestal is a protected area of forest of the type characteristic of the plateau of the southern part of the state of São Paulo. The terrain consists of alternating hills and ravines; the parts chosen for experimental fields are covered with fairly dense forest composed of many species of trees and some lianas and epiphytes. *Hairless* flies were raised in the laboratory under optimal conditions, counted without etherization, aged for from 3 to 6 days after hatching, and released at a point previously chosen on the experimental field for furnishing some protection to the flies immediately after their liberation (shade and a cover of fallen leaves on the ground). The experimental field was then left undisturbed for one or several days.

To study the distribution of the wild and of the released flies on the experimental field, bait was placed at ten-meter intervals along two lines intersecting, at the point of release, approximately at right angles. Each bait consisted of about half a kilogram of fermenting banana placed directly on the ground or on the fallen leaf cover. The experimental fields were, therefore, cross-shaped, each arm of the cross consisting of regularly spaced bait, with the point of release (also baited) at the center. The flies are caught by rapid strokes of a collecting net in the air above the bait, transferred into numbered glass vials, etherized, classified and counted under a binocular microscope in the field. The collections are repeated at about one hour intervals during most of the day; equal numbers of collections are made on all baits.

First Experiment

At 5 P.M. on December 3, 1948, 4,330 *hairless* flies were released at Cantareira. On December 6, 29 baits spaced at 10-meter intervals were placed along two intersecting lines. The bait at the point of release was designated No. 0. Baits No. 1–7, 0, and 8–14 formed one line, and No. 15–21, 0, and 22–28 formed the other line. Baits No. 1, 14, 15, and 28 were, therefore, 70 meters distant from the point of release, while No. 7, 8, 21, and 22 were 10 meters distant. A summary of the collection records is presented in table I. A total of 259 *hairless* and 65 wild *D. willistoni* flies, and 327 individuals of other species of Drosophila, were captured.

Inspection of table I shows that *hairless* flies were most frequent at the point of release (41 on bait No. 0), somewhat less frequent 10 meters away from that point (baits No. 7, 8, 21 and 22 with 16, 25, 38 and 32 *hairless* flies respectively), while only 3 *hairless* flies were found 70 meters away from the point of release. If the flies disperse uniformly in all directions on the experimental field, they should show a normal probability distri-

TABLE I. *Numbers of released and of wild* Drosophila willistoni, *as well as of other species of Drosophila, found on the experimental field in the first experiment*

Bait no.	*willistoni* hairless	*willistoni* wild	*medio-*	*guara-munu*	*griseo-lineata*	*capri-corni*	*bocai-nensis*	*simulans*	*poly-morpha*	Others
1	1	3	3	—	—	—	—	—	—	—
2	4	4	2	—	—	—	1	—	—	—
3	4	—	—	—	—	—	1	—	—	1
4	2	1	—	—	2	5	1	—	—	—
5	10	1	1	—	—	1	—	—	—	—
6	12	4	2	—	1	—	—	—	—	—
7	16	3	2	1	—	2	1	—	—	—
0	41	4	5	2	2	2	—	1	—	1
8	25	1	3	—	2	1	—	2	1	3
9	10	3	23	3	—	—	—	—	—	—
10	3	3	6	5	3	—	1	—	—	3
11	1	1	16	4	1	1	—	1	—	3
12	2	—	3	—	—	—	2	—	—	—
13	—	2	2	—	—	—	—	—	—	—
14	—	1	7	—	—	—	—	—	—	—
.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
15	—	7	3	—	—	1	—	—	1	—
16	2	3	1	—	—	—	—	—	1	1
17	1	1	10	—	—	4	1	—	1	—
18	5	1	4	2	2	—	3	—	1	1
19	9	2	24	6	—	1	2	—	—	—
20	22	2	3	—	—	2	1	—	—	1
21	38	1	12	6	6	6	1	—	1	—
22	32	7	2	6	—	3	1	2	1	—
23	6	—	14	2	4	4	2	—	2	1
24	2	3	10	—	—	2	—	—	—	—
25	3	2	5	—	1	2	1	—	1	—
26	3	2	3	—	—	2	—	—	—	—
27	3	2	4	—	—	2	—	—	—	—
28	2	1	5	—	—	—	—	—	—	—
Total	259	65	175	37	24	41	19	6	10	15

bution centered on the point of release. Their distribution can, then, be characterized by the variance of the distances from the point of release, at which the *hairless* flies are found on the experimental field at a given time (Dobzhansky and Wright, '43, '47). This variance, σ^2, is the sum of squared distances, divided by the number of flies

$$\left(\frac{\Sigma r^2 f}{n+c}\right).$$

In this and the following formulae, r is the distance at which a fly is found from the point of release, f is the frequency of such flies, n is the total number of *hairless* flies found, and c is the number of *hairless* flies found on the bait at the point of release; c is added to n because the bait at the point of release (No. 0) is a part of both intersecting bait lines. The variance computed from data in table I is 475 square meters.

This variance, however, does not give a satisfactory description of the observed distribution of *hairless* flies on the experimental field, because their distribution does not follow a normal probability curve but is leptokurtic, i.e., shows an excessive accumulation at the center and excessive scattering toward the ends of the bait lines. The kurtosis is measured by a ratio of the fourth moment (sum of fourth powers of the distances from the point of release divided by the number of flies) to the square of the second moment (sum of second powers divided by the number of flies). In a normal curve this ratio is 3, while it is 4.56 for the distribution of *hairless* flies in the experiment under consideration. The kurtosis is not accidental, since leptokurtic distributions of the

released flies have been observed in all experiments on *D. pseudoobscura* (Dobzhansky and Wright, '43, '47; Bateman, '49). The origin of the kurtosis is not clear; it may arise if some of the released flies are stimulated to take at least one long flight while most flies disperse at slower rates; it may come about also if some of the flies are weak and are unable to move at normal speed. The best available measure of the dispersal of flies in a leptokurtic distribution is the variance of the distances from the point of release of the whole population of *hairless* flies in a single direction, which can be obtained by calculating $\Sigma r^3 f/2(\Sigma rf + c/8)$. This formula, generously supplied by Professor Sewall Wright, represents an improved version of that given on p. 312 of the Dobzhansky and Wright, 1947, paper. The variance so computed is 644 meters^2, which is appreciably higher than the first estimate given above.

The distribution of *hairless* flies on the experimental field characterized by the above variance is a result of the dispersal of the flies during two and a half days following their release (December 4, 5, about half of December 6) when the collecting was being made, and some two hours on the afternoon of December 3; only daylight hours need be considered since the flies are quiescent at night (see Pavan, Dobzhansky, and Burla, '50). Now, if *D. willistoni* moves at random in a uniform environment, as *D. pseudoobscura* is known to do, the variance increases in proportion to the time elapsed after the release. Therefore, it is convenient to describe the dispersal of the flies in terms of increment of variance per day, which in our case is about 258 meters^2.

Table I shows that 65 wild *D. willistoni* flies were captured together with the 259 *hairless* flies. On the assumption that wild and *hairless* flies are attracted to the bait to about the same extent, the data permit computation of the density of the population of wild flies on the experimental field. We are greatly indebted to Professor Sewall Wright for the following formula for this computation:

$$\text{wild flies per 100 meters}^2 = \frac{f_w N \times 0.9^t}{2\pi(\Sigma r f_r + 1/8c)}$$

where f_w and f_r are the numbers of wild and of *hairless* flies respectively found at each collecting point (bait), N is the number of released *hairless* flies (4,330), t is the number of days intervening between release and collecting, and c and r have the same significance as before.[2] For the data at hand, the computation gives a population density of 10.04 wild *D. willistoni* flies per 100 m^2.

Representatives of eleven species of Drosophila were found together with wild and *hairless* *D. willistoni* on the experimental field. These are: *D. guaramunu* Dobzhansky and Pavan, *D. griseolineata* Duda, *D. capricorni* Dobzhansky and Pavan, *D. bocainensis* Pavan and da Cunha, *D. simulans* Sturtevant, *D. polymorpha* Dobzhansky and Pavan, *D. guarani* Dobzhansky and Pavan, *D. fumipennis* Duda, *D. prosaltans* Duda, at least one species related to *D. calloptera* Schiener, *D. mediostriata* Duda, *D. mediosignata* Dobzhansky and Pavan, and *D. mediopunctata* Dobzhansky and Pavan. The three last named species, and possibly some related undescribed forms, are difficult to distinguish, and accordingly are combined in table I and the subsequent ones in the column marked "medio." More important still for our present purpose is that the flies classified as wild *"D. willistoni"* are in fact also a mixture of two species which are morphologically distinguishable with difficulty, namely, *D. willistoni* Sturtevant and *D. paulistorum* Dobzhansky and Pavan (Burla, da Cunha, Cordeiro, Dobzhansky, Malogolowkin, and Pavan, '49). The figures for population density are, then, referable to the two species

[2] This formula is an improved version of the one given by Dobzhansky and Wright ('47, p. 314). In the latter paper, the summation sign, Σ, was inadvertently omitted before the rf_r symbol.

jointly. The relative frequencies of these species vary with the season, the true *D. willistoni* being more common during the cool and *D. paulistorum* during the hot season. For our data we may accept the figure one-third as being a fair estimate of the frequency of *D. willistoni,* and two-thirds for *D. paulistorum.*

Since different species of Drosophila are not attracted to banana bait to the same extent, the distribution of *hairless D. willistoni* flies cannot be relied upon for estimation of population densities of other species. It may nevertheless be conjectured that the reactions of *D. willistoni* to banana bait are somewhere near the average for Drosophila species. If this is the case, since 65 wild *D. willistoni* and *D. paulistorum* have been captured among 392 individuals of all species, one can estimate the population density of all Drosophila flies on our experimental field as close to 60 per 100 m².

Second Experiment

4,700 *hairless* flies were released at 8 A.M. on December 28, 1948, at a point about one kilometer from the center of the experimental field used in the first experiment. The collecting was made on December 29, with 41 banana baits spaced at 10-meter intervals in two lines intersecting at the point of release. One line, 200 meters long, consisted of baits No. 1–10, 0 (center), 11–20; the baits No. 21–30, 0, 31–40 formed the other, equally long, line. The baits No. 1, 20, 21, and 40 were, accordingly, 100 meters away from the point of release. The results of collecting are summarized in table II; 326 *hairless* and 368 wild *D. willistoni* and *D. paulistorum* flies and 1,289 individuals of other species of Drosophila were recorded. Among the latter, *D. nebulosa* Duda, *D. sturtevanti* Duda, *D. dreyfusi* Dobzhansky and Pavan, a species of the *D. repleta* group, as well as all species recorded in the first experiment (see above) were found.

The distribution of *hairless* flies showed, as expected, a maximum in the vicinity of the point of release (bait No. 0), while none were found on baits 100 meters away. The variance of the distribution of *hairless* flies along the lines of bait is 907 meters². The distribution of *hairless* is, however, leptokurtic, as it was in the first experiment (kurtosis 4.27). It is, therefore, necessary to compute the variance of the distances of the whole population in one direction (see above), which turns out to be 1,272 meters². Since in the second experiment the flies were collected on the average one and one-half days after the release, the increment of variance per day is only 828 meters². This figure, it may be noted, is more than three times as high as the comparable estimate obtained in the first experiment (258 m²). The difference is doubtless due to the higher temperatures which prevailed during the second experiment (see below).

Table II shows that 368 wild *D. willistoni* and *D. paulistorum* were found together with the 326 recaptured *hairless* flies. With the aid of the formula given above, the population density of wild *D. willistoni* on the second experimental field is estimated as 28.2 flies per 100 meters². This is about three times as high a density as found on the first experimental field some three and a half weeks earlier. Examination of table II shows, however, that this discordance is not unexpectedly high. Indeed, neither the wild *D. willistoni* nor other species are uniformly distributed over the field. The population density of wild *D. willistoni* was much higher in the vicinity of the baits No. 16–20 (which were located in a humid ravine) than near No. 1–6 (hill slope) and No. 31–36 (dense forest). *D. griseolineata* and *D. guaramunu* showed high densities in the neighborhood of the point of release, while species of the *medio-* group formed a peak at the center and near the baits No. 32–40 (dense forest). Such non-uniformities in the distribution of wild flies have been observed by the Timofeeff-Ressovskys ('40) for *D. melanogaster, D. funebris,* and for spe-

TABLE II. *Numbers of released and of wild* Drosophila willistoni, *as well as of other species of Drosophila, found on the experimental field in the second experiment*

Bait no.	*willistoni* hairless	*willistoni* wild	*medio-*	*guara-munu*	*griseo-lineata*	*capri-corni*	*bocai-nensis*	*simulans*	*poly-morpha*	Others
1	—	8	12	—	—	3	4	1	—	—
2	—	4	7	1	—	1	—	—	—	1
3	2	1	10	—	1	—	—	1	1	—
4	1	1	5	1	2	1	1	2	—	1
5	1	8	3	1	1	—	1	—	—	3
6	—	3	7	—	—	1	4	—	—	—
7	5	6	24	2	—	—	14	1	—	—
8	9	8	35	11	15	4	10	1	1	1
9	13	10	31	23	44	1	5	—	—	2
10	20	3	21	8	12	3	1	2	—	1
0	58	11	11	9	9	—	6	—	—	1
11	18	7	14	6	1	—	3	—	2	—
12	13	6	15	3	—	2	5	—	—	—
13	10	14	21	8	4	3	3	—	—	1
14	5	3	7	—	—	—	3	—	1	2
15	4	2	4	1	—	—	3	1	—	2
16	—	12	9	1	—	1	2	1	1	1
17	4	16	9	—	1	3	—	8	—	3
18	4	10	7	2	—	2	12	4	1	2
19	5	34	3	—	—	5	10	2	—	—
20	—	66	6	1	—	7	4	5	—	4
.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
21	—	5	2	—	—	11	2	4	—	4
22	1	3	1	2	1	5	1	2	—	1
23	—	3	—	—	—	1	1	—	—	1
24	4	12	4	—	—	1	2	3	—	1
25	3	4	3	—	—	1	2	1	—	2
26	11	15	5	—	—	2	2	5	—	5
27	6	7	—	—	—	—	—	4	1	1
28	19	2	2	1	1	1	1	4	1	1
29	19	12	13	10	6	2	2	6	—	2
30	39	9	2	8	8	4	2	—	2	1
31	12	4	11	9	9	2	1	—	—	1
32	8	4	32	8	13	2	2	—	—	—
33	12	2	16	11	7	4	2	—	—	3
34	4	4	23	3	—	2	3	—	—	—
35	7	8	43	9	16	4	5	1	1	1
36	5	4	52	3	10	—	3	1	—	1
37	3	12	13	3	1	4	—	—	—	4
38	—	11	41	—	—	—	—	—	—	3
39	1	4	56	—	—	1	2	—	—	1
40	—	10	62	1	—	1	—	—	—	—
Total	326	368	642	146	162	85	124	60	12	58

cies of the *D. obscura* group, and by Dobzhansky and Wright ('43, '47) for *D. pseudoobscura* and its relatives. We hope to show in another publication that such aggregations of representatives of species of Drosophila in different neighborhoods in the same general habitat reflect differences in environmental preferences of these species, particularly in food preferences. It is interesting to note that some species (*D. pseudoobscura, D. obscura*) are distributed relatively more uniformly than others (*D. melanogaster* and most of the species in tables I–IV of the present paper). This may reflect a greater mobility of the former as compared to the latter, as well as relative promiscuity *vs.* specialization of the environmental preferences. The importance of this aggregation phenomenon in connection with population density determinations lies in that such determinations represent merely averages for a given experimental field, and hence are expected

to vary greatly depending upon whether nuclei of high concentration of a species happen to be included in such a field.

The 368 wild *D. willistoni* listed in table II were found among 1,657 wild Drosophila of all species; *D. willistoni* and *D. paulistorum* constituted, accordingly, about 22 per cent of the total Drosophila catch. With reservations stated in connection with similar calculations based on the data of the first experiment (see above), one arrives at the estimate of about 128 individuals of all species of Drosophila per 100 meters^2 on the second experimental field. This is slightly more than twice the estimate arrived at in the first experiment. Since the terrain of the second field is in general more favorable for Drosophila than that of the first (a greater abundance of large trees and a better protection from the wind), and in view of what has been said in the preceding paragraph regarding local aggregations in Drosophila, the two estimates may be considered to stand in fair agreement.

TABLE III. *Numbers of released and of wild* Drosophila willistoni, *as well as of other species of Drosophila, found on the experimental field in the third experiment*

Bait no.	*willistoni* hairless	*willistoni* wild	*medio-*	*capricorni*	*bocainensis*	*bandeirantorum*	*ismulans*	*polymorpha*	*guaramunu*	*calloptera*	Others
1	—	7	10	6	2	2	—	—	1	—	—
2	—	4	25	4	1	—	—	—	—	1	1
3	—	—	13	3	3	1	—	—	—	2	—
4	—	3	21	—	3	4	—	1	1	1	1
5	—	1	27	8	2	2	2	—	—	1	—
6	1	3	32	6	4	7	—	—	—	—	1
7	1	4	35	9	4	2	—	—	3	—	—
8	7	3	38	1	7	3	1	—	—	—	—
9	17	11	49	23	3	12	2	2	—	—	—
10	21	1	15	4	3	2	—	—	—	—	1
0	40	9	43	8	2	11	—	2	1	6	1
11	19	3	8	1	2	3	2	—	—	—	—
12	7	3	8	2	—	2	—	—	—	2	—
13	24	13	32	9	—	1	2	—	1	—	1
14	3	1	4	3	—	4	—	—	—	3	2
15	2	—	3	1	—	—	—	—	—	—	1
16	1	—	5	—	—	1	1	—	—	—	—
17	1	4	2	2	—	2	1	—	—	—	2
18	—	2	5	2	1	2	3	—	—	—	1
19	—	1	14	—	—	1	—	—	—	—	9
20	—	9	7	4	2	1	4	—	—	—	2
21	—	1	23	1	1	2	—	—	—	—	1
22	—	10	23	6	3	1	2	—	—	—	3
23	1	15	32	4	—	—	2	—	—	1	5
24	1	7	18	4	—	—	—	—	—	—	4
25	4	15	15	4	2	2	3	—	2	—	3
26	8	21	14	6	1	2	6	1	5	—	1
27	6	2	1	5	—	1	—	—	—	—	1
28	26	3	7	4	—	2	—	—	—	—	—
29	24	6	5	6	—	2	—	—	1	—	1
30	18	1	3	2	—	—	1	—	—	—	—
31	9	—	14	2	—	1	2	1	—	—	4
32	7	—	12	1	—	2	—	—	1	—	3
33	1	2	8	—	—	1	—	—	—	—	—
34	—	—	32	8	1	2	—	—	—	—	—
35	—	1	47	17	—	2	—	—	—	—	2
36	1	2	38	2	—	4	1	—	—	—	3
37	—	1	17	4	—	3	—	—	—	2	3
38	—	1	18	3	—	2	—	—	—	1	—
39	—	1	36	3	—	1	2	—	1	3	2
40	—	2	44	2	—	—	3	—	2	6	2
Total	250	173	803	180	47	93	40	7	19	29	61

Third Experiment

At 9 A.M. on June 9, 1949, 4,154 *hairless* flies were released at the same point at which the flies were liberated in the second experiment, made five and a half months earlier (see above). The collecting of the flies was performed on June 11, the 41 baits having been placed at the same points as in the second experiment. Using the same experimental field twice was regarded as safe because few, if any, homozygous *hairless* flies could be expected to persist on the experimental field for several months (cf. Dobzhansky and Wright '47). The results of collecting are reported in table III; 250 *hairless* and 173 wild *D. willistoni* flies, and 1,279 flies of other species of Drosophila have been recorded.

Although *hairless* flies were more frequent at the point of release than elsewhere, the distribution of *hairless* is somewhat asymmetrical: the four arms of the cross-shaped field gave 47, 57, 88, and 18 *hairless* respectively. The Timofeeff-Ressovskys ('40) observed asymmetrical distributions of recaptures of released *D. melanogaster* and *D. funebris,* and ascribed the asymmetry to wind. There is no basis for such an interpretation in the present experiment. Dobzhansky and Wright ('43, '47) found no wind effects in experiments with *D. pseudoobscura,* but did observe that released flies tend to congregate at points which are also attractive to wild flies of the same species (old trees, etc.). Examination of table III likewise discloses that the smallest number of *hairless* were found along the arm of the cross which had fewest wild *D. willistoni,* and vice versa.

The variance of the distribution of *hairless* flies along the lines of bait is 559 meters^2, and the variance in one direction 647 meters^2. The kurtosis is only weakly pronounced ($k = 3.5$). Two and a half days elapsed between the release and the average time of collecting of flies in the third experiment. The increment of variance per day is, accordingly, 259 meters^2. This is almost identical with the estimate derived from the first experiment (258 meters^2). Since the first and the third experiments were carried at similar temperatures (see below), the variances are expected to be similar, but the very close agreement obtained is, of course, accidental.

The population density of wild *D. willistoni* and *D. paulistorum* turns out to be 16.6 flies per 100 meters^2. This can be compared with the estimate of 28.2 flies per 100 meters^2 obtained on the same experimental field in the second experiment conducted some five and a half months earlier. The abundance of a species from season to season, as well as in different microenvironments, varies greatly in tropical forests, as we hope to show in another publication. Since the 173 wild *D. willistoni* in the third experiment were found amongst 1,452 individuals of all species of Drosophila, the aggregate population density may be close to 139 flies per 100 m^2.

Fourth Experiment

At 11 *a.m.* on July 2, 1949, 5,505 *hairless* individuals were released at Cantareira, at a point about one kilometer distant from the experimental fields used in the preceding experiments. On July 4, 41 baits were placed at 10-meter intervals in two lines intersecting at the point of release, as usual. Table IV shows a summary of the results; 240 *hairless* and 88 wild *D. willistoni,* and 2,031 flies of other species of Drosophila were captured. The number of species was 15, among them *D. annulimana* Duda and *D. pulla* Pavan and da Cunha, which were not recorded in the preceding experiments.

Of the 240 *hairless* flies, 195 were found at the point of release. Nevertheless, 5 *hairless* flies were captured 50 to 80 meters from this point. The distribution of *hairless* is sharply leptokuric (kurtosis 46.0). It is evident that, owing to the low temperatures that prevail, a majority of the released flies failed to move away from the point of release.

TABLE IV. *Numbers of released and of wild* Drosophila willistoni *and of other species of Drosophila found on the experimental field in the fourth experiment*

Bait no.	*willistoni* hairless	*willistoni* wild	*medio-*	*capri-corni*	*bocai-nensis*	*bandei-rantorum*	*poly-morpha*	*calloptera*	*guarani* group	*griseo-lineata*	Others
1	—	6	27	5	—	5	—	1	—	—	—
2	—	—	—	—	—	—	1	1	—	—	—
3	—	4	32	12	1	—	1	—	—	1	—
4	—	2	24	5	—	1	3	—	1	—	—
5	—	—	40	8	—	—	1	1	—	3	—
6	1	2	63	4	1	4	1	—	—	5	1
7	1	5	37	3	1	2	—	—	—	1	1
8	—	4	28	5	2	—	—	1	—	—	—
9	3	1	48	10	4	2	—	2	—	—	—
10	9	2	31	13	4	2	1	—	—	—	—
0	195	6	28	12	4	2	—	2	—	—	—
11	2	—	38	4	2	—	1	3	—	—	—
12	—	2	62	—	2	—	1	2	—	—	—
13	1	—	37	2	4	—	—	—	—	2	—
14	—	—	21	2	3	—	—	—	—	—	—
15	—	2	18	—	—	—	—	—	—	—	1
16	—	5	56	15	2	2	—	2	—	—	—
17	—	3	31	21	1	4	—	—	1	—	—
18	—	6	50	2	—	—	—	1	—	2	—
19	—	4	64	8	1	10	—	2	2	1	2
20	—	2	51	7	—	1	—	—	—	1	—
21	—	4	48	—	—	—	—	3	1	—	—
22	—	—	27	1	—	—	—	—	—	—	—
23	—	—	23	3	—	—	—	2	—	—	—
24	1	1	50	2	1	—	—	5	—	2	—
25	1	—	25	2	2	—	1	2	—	—	—
26	—	1	34	10	5	—	—	—	—	—	—
27	—	—	24	4	4	—	—	—	—	—	—
28	1	3	55	6	5	—	—	—	—	—	—
29	1	1	49	16	4	5	—	2	2	1	4
30	14	5	80	20	8	1	—	4	—	1	—
31	4	6	31	12	2	—	1	1	1	—	1
32	3	2	39	2	1	2	2	1	1	—	—
33	—	1	24	2	5	—	1	1	2	—	—
34	1	1	25	—	—	—	—	—	2	—	1
35	—	3	9	4	2	—	1	1	—	1	2
36	—	—	15	1	1	1	1	1	3	—	—
37	1	1	22	2	2	1	2	—	1	—	—
38	1	—	63	3	2	—	1	3	1	—	—
39	—	—	75	2	1	—	1	2	1	—	—
40	—	—	45	2	—	1	1	2	1	—	—
Total	240	88	1,549	232	77	46	22	48	20	21	15

Numerous *hairless* flies were, in fact, observed on the ground and on fallen leaves in the immediate vicinity of the point of release (within a meter). Moreover, these flies were in a kind of stupor, so that sweeping with a collecting net in the air above them failed to stimulate them to fly upward, as flies normally do at higher temperatures. There can be no doubt that the 195 *hairless* flies recorded at the point of release represent only a fraction of the flies that remained there for two days after their release.

Nevertheless, some flies did make rather long flights, as shown by the finding of two flies at 40 and at 70 meters, and of single flies at 50, 60, and 80 meters from the point of release. It is this minority, probably a small minority, of the flies that is responsible for the extremely leptokurtic distribution observed among *hairless* flies. Calculation of variance along the lines of bait gives 76 meters^2. Little confidence can be placed on this estimate, and even less can be placed on the estimate of the variance in one direction,

since the magnitude of these constants in a sharply leptokurtic distribution depends too much on the very few individuals captured far from the point of release. All that the fourth experiment really shows is that at the low temperatures which prevailed at Cantareira between July 2 and July 4, *D. willistoni* flies remain mostly inactive, in other words, that these temperatures are close to the limit below which this species remains stationary, or at least does not make long flights.

Discussion

Dobzhansky and Wright ('43, '47) showed that the dispersal rates in *Drosophila pseudoobscura* are strongly influenced by temperature conditions. The same is evidently true for *D. willistoni*. Through the courtesy of the Instituto Regional de Meteorologia in São Paulo as well as of Dr. Mansuet Kozinski of the Horto Florestal at Cantareira, we have obtained the following summary of the temperature data (in C.°) for the days when our experiments were in progress:

Experiment	Date	Maximum	Minimum	Mean
First	December 4, '48	20.0	15.4	18.7
	December 5, '48	23.6	14.3	18.7
	December 6, '48	28.0	10.9	21.4
Second	December 28, '48	33.5	12.2	25.5
	December 29, '48	28.3	16.9	23.0
Third	June 9, '49	23.0	11.4	17.8
	June 10, '49	25.1	14.1	18.8
	June 11, '49	21.5	13.3	17.2
Fourth	July 2, '49	18.7	7.9	13.0
	July 3, '49	21.7	5.6	13.7
	July 4, '49	?	6.3	16.7

As explained above, the dispersal rates of the flies are measured in terms of the increment of variance per day (in square meters); with the two methods of calculation used, the results are as follows:

Experiment	Variance along the lines of bait	Variance in a single direction
1st	190	258
2nd	605	828
3rd	254	259
4th	30 (?)	?

The dispersal rates are obviously much higher at warm than at cool temperatures. According to Dobzhansky and Epling ('44) and Dobzhansky and Wright ('43), the Californian *D. pseudoobscura* remains inactive when the temperature during the hours when it might otherwise be flying falls below 13°. This is only slightly lower than the mean temperature which prevailed during our fourth experiment with *D. willistoni*, when the flies showed little activity.

Comparison of the dispersal rates of the two species is, however, made difficult by the fact that *D. willistoni* is more or less active at all daylight hours, while, *D. pseudoobscura* flies only in the morning and in late afternoon (Pavan, Dobzhansky, and Burla, '49; Dobzhansky and Epling, '44). Thus, on July 4 it was noted that flies came to bait chiefly during early afternoon when the temperature reached its maximum for the day. Thus, while the dispersal rates of *D. pseudoobscura* can easily be correlated with temperatures at the time of its greatest activity, it is open to question whether the dispersal rates in *D. willistoni* are influenced more by temperature conditions during the morning, midday, afternoon, or even night. The following are very rough estimates of the increment of variance in a single direction per day, derived from the data of Dobzhansky and Wright ('43, '47) for *D. pseudoobscura*:

Experimental field	Temperature range	Variance in meters² per day
San Jacinto I	14°–19°	1500
San Jacinto II	19°–21°	4000
San Jacinto III	21°–25°	6000
San Jacinto IV	21°–26°	8000
Mather	21°–22°	8000

Despite the difficulty of making exact comparison of dispersal rates of different species, it is abundantly clear that the increments of variance observed in *D. pseudoobscura* are of a higher order of magnitude than those in *D. willistoni*. So great a difference in dispersal rates must have important consequences for the population structure of the species. Other things, such as population density and mating habits, being equal, *D. willistoni*

would have a lower genetically effective population size, and consequently more differentiation into local races, than *D. pseudoobscura.*

The data of the Timofeeff-Ressovskys ('40) indicate that the dispersal rates in *D. melanogaster* may be of the same order of magnitude as in *D. willistoni* or even lower, although no numerical estimates, even as imperfect as the above, may be obtained from their data. It may be noted that *D. melanogaster* and *D. willistoni* are species of subtropical or tropical origin, although the former has become almost cosmopolitan through association with man; *D. pseudoobscura* is, on the contrary, a temperate zone species which occurs in the Tropics (Mexico, Guatemala) only at high elevations. It is, however, premature to speculate about the possible relations between the dispersal rates and the tropical or temperate zone distributions.

The densities of populations of *D. willistoni* (and *D. paulistorum*) on our experimental fields have been estimated between 10 and 28 individuals per 100 meters^2, and those of all species of Drosophila, less reliably, between 60 and 139 flies per 100 meters^2. Judging by the numbers of flies that were being caught on these experimental fields and the numbers collected on our excursions in various parts of Brazil, the above population densities are by no means the highest that occur in tropical forests. Populations that are certainly tens, and possibly hundreds of times more dense were found, for example, on some islands in lower Rio Negro in late April, 1949.

In contrast to this, population densities of *D. pseudoobscura* in California mountain forests varied from 0.9 to about 10 flies per 100 meters^2 (Dobzhansky and Wright, '47).[3] No counts of other species of Drosophila were made in the California experiments, but it may be noted that *D. pseudoobscura* is usually by far the commonest species in California forests. It is clear, then, that Drosophila species reach higher aggregate population densities in tropical forests in Brazil than in the forests of California. The number of species of Drosophila is, however, appreciably greater in Brazil than in California, and some of these species are relatively rare at some or at all seasons of the year. As a result, it is probable that there exists a greater range of population densities among tropical than among temperate Drosophilae. Among Brazilian species, *D. willistoni* is one which often has very high population densities. It is also a species characterized by a great ecological versatility, which permits it to flourish in almost all parts of Brazil where we have collected Drosophila material (except in the "caatingas" in the valley of Rio São Francisco, state of Bahia, where we found *D. willistoni* a rare species in late February, 1949). In many places, it is the dominant species of Drosophila. The high population densities make *D. willistoni,* despite its relatively low dispersal rates, a species with high genetically effective population sizes. This conclusion is confirmed by studies on the incidence of recessive autosomal lethals and of other genetic variants in *D. willistoni,* which will be reported in other publications.

Acknowledgments

This work, carried out in the laboratory of Professor Andre Dreyfus at the University of São Paulo, was supported in parts by grants made by the Rector of that university, Dr. Linneu Prestes, by the Rockefeller Foundation, and by the Carnegie Institution of Washington. Dr. Edmundo Nonato, Mrs. Anita Burla, and the Misses Elisa Nascimento Pereira, Marta Wedel, and Sophia Dobzhansky

[3] The estimate of 0.9 fly per 100 m.^{2}, obtained at Mather, California, refers to the combined densities of three closely related species, *D. pseudoobscura, D. persimilis* and *D. azteca.* Of this number, only 0.4 belongs to *D. pseudoobscura.* Higher estimates were obtained in several experiments on Mount San Jacinto, where *D. pseudoobscura* is the only species of this group.

have kindly assisted in collecting the flies on the experimental fields. The administration of the Horto Florestal, Cantareira extended to us the facilities of their Institution. To Professor Sewall Wright of the University of Chicago, we owe many invaluable suggestions regarding the mathematical analysis of the data.

Summary

Known numbers of the *hairless* mutant of *Drosophila willistoni* were released at certain points in a forest in the neighborhood of São Paulo. One or more days after the release, Drosophila flies were collected on bait placed at various distances from the point of release, and the numbers of the *hairless* and of wild individuals caught were recorded. Four experiments of this kind were made at different temperature conditions.

The dispersal rates of *D. willistoni* vary greatly with temperature. They are consistently of a lower order of magnitude than those found by Dobzhansky and Wright ('43, '47) for *D. pseudoobscura* in California.

The densities of wild populations of *D. willistoni, D. paulistorum* and of other species are far from uniform in space; nuclei of high and of low concentration may exist within a few meters of each other. The average population densities of *D. willistoni* on our experimental fields have varied from about 10 to 28 flies per 100 square meters, and of all species of Drosophila from about 60 to 139 flies per 100 square meters. These population densities are appreciably higher than those found for *D. pseudoobscura* in the most favorable seasons in California forests.

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THE NET PHYTOPLANKTON OF QUABBIN RESERVOIR, MASSACHUSETTS, IN RELATION TO CERTAIN ENVIRONMENTAL FACTORS

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Several investigators (Kofoid '03, Allen '20, Pearsall. '23a) have observed distinct pulsations in populations of phytoplankton and have attributed the periodicities to various physical and chemical factors. For purposes of possible comparisons with similar studies of other bodies of fresh water it was deemed advisable to institute a survey of the net phytoplankton of Quabbin Reservoir in central Massachusetts. The artificial nature and recent construction of the reservoir, together with its large area, afford excellent opportunity for collecting these organisms in a protean situation.

FEATURES OF QUABBIN RESERVOIR

Quabbin Reservoir, located in central Massachusetts, is an artificially created body of water which covers an area of 38.6 square miles. The reservoir commenced filling in August 1939 and reached its capacity of 415 billion gallons in the spring of 1946. During the seven-year period of filling, a continuous flow of 20 million gallons per day was released downstream to the old river bed (Swift River), and an average of approximately 39 million gallons per day was drawn for consumption in the Metropolitan District (Greater Boston).

There are over 177 miles of shore line to the reservoir whose greatest length exceeds 18 miles. Over 100 islands dot its waters. The maximum depth is 148 feet and the average depth is more than 50 feet. The elevation of the spillway is 530 feet above sea level.

[1] The author is indebted to Prof. A. V. Osmun and Dr. T. T. Kozlowski, of the Botany Dept., Univ. of Mass., and to Dr. H. J. Oosting, of the Botany Dept., Duke Univ., for their advice and assistance in the preparation of the manuscript.

In preparation of this reservoir, the bottom was not stripped of top soil, though it was cleared of all woody and much of the herbaceous vegetation to an elevation above the shore line.

The main tributaries to Quabbin Reservoir are the three branches of the Swift River (fig. 1). Before their courses were altered these rivers flowed southward through Quabbin Valley, part of which now lies below the surface of the reservoir. This entire natural depression extends from above the New Hampshire border on the north to approximately the Connecticut line on the south. The Pelham-Shutesbury-Wendell hills compose the valley's western limit, while on the east, Quabbin Valley is bounded by an elevation extending from Ware northward through Hardwick to Phillipston and Royalston.

Geologically the substratum of the valley is quite uniform. The eastern and western slopes consist largely of biotitic granite and biotitic gneissoid granite. Graphitic, biotitic, and feldspathic schists compose the sedimentary rocks which underlie the northern extremity of this valley. The "floor" is of igneous rocks including gneissoid grandiorite, diorite, and aplite. Other igneous rocks in the vicinity that could conceivably affect the character of the water are pegmatite and peridotite (Emerson '17).

The plant communities adjacent to the reservoir are of two general types; the bog associations and the pine-spruce associations. In the acid bogs to the north of Quabbin are found the Sphagnum-Chamaedaphne and Tamarack-Black Spruce associes. Here, also, are found other heaths (Vaccinium, Kalmia, etc.). Prior to the creation of this reservoir by

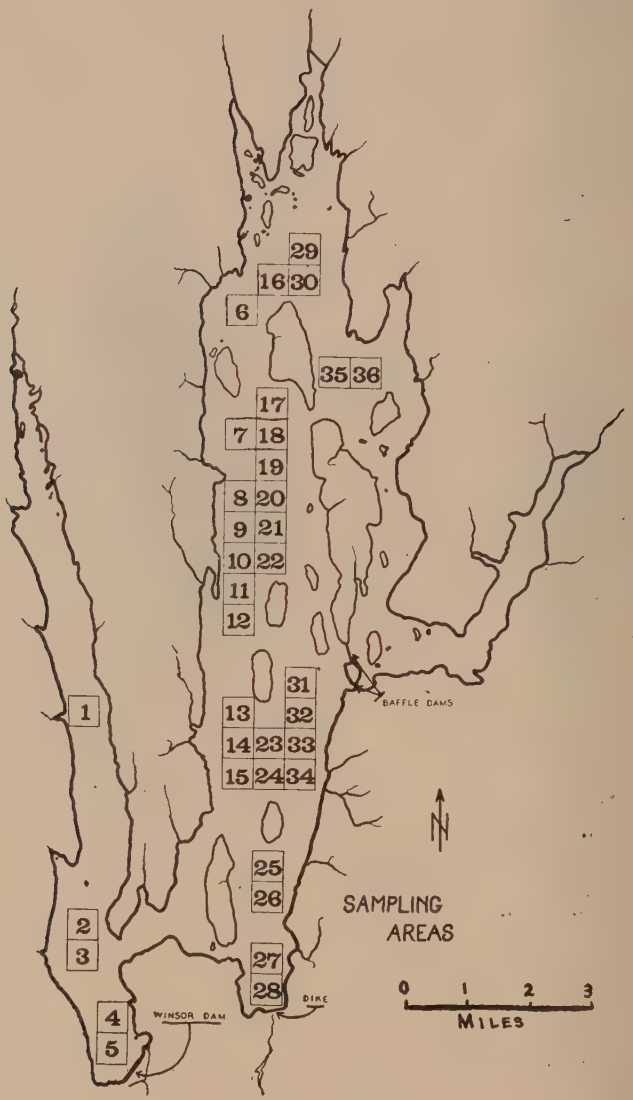

FIG. 1. Map of Quabbin Reservoir showing location of sampling areas (numbered).

The Commonwealth of Massachusetts, Quabbin Valley supported many farms, but the abandonment of this land has allowed it to revert to pine (*Pinus strobus*). Large areas of the former farm land also have been planted to pine (*Pinus strobus, Pinus resinosa*) and spruce (*Picea sp.*). The willow (*Salix* sp.)–alder (*Alnus incana*)–hornbeam (*Carpinus caroliniana*) associes are commonly found along Quabbin's tributaries.

REVIEW OF LITERATURE

Of the numerous physical and chemical conditions that appear to have an influence on phytoplankton abundance, wa-

ter temperature is that factor which has been demonstrated most frequently as affecting population pulses (Kofoid '08, Allen '20, Eddy '27a). Both Daily ('38) and Damann ('41) conclude that temperature has a pronounced effect upon the total phytoplankton but it is not the sole determining factor of periodicity. Pearsall ('23a) minimizes the role of temperature in plankton diatom abundance, but is inclined to believe that deficiencies of oxygen, nitrate, silica, and calcium are the usual limiting factors. In a recent exploration of the plankton and its relationship to environmental factors, Hupp ('43) found no correlation between increase of water temperature and abundance of plankton during late spring and summer. However, during the early spring, previous to any plankton pulse, there were often minor population fluctuations which ran parallel with changes in water temperature.

These effects of temperature on microorganisms are direct; but the indirect effects, as pointed out by Patrick ('48) for plankton diatoms, are equally if not more important. Water temperature not only affects solubility of salts and gases but also spring and fall overturns, melting of snow and ice, and thus the supply of nutrients.

As with higher plants, there are some species of the phytoplankton which grow well in abundant light, while others live in regions of low light intensity (Patrick '48). In the Ohio River, Purdy ('22) found that holophytic organisms are dependent upon sunlight for maximum growth. Goudey ('38) indicates that in California there is a direct relationship of phytoplankton multiplication to the ultra-violet radiation in sunshine. Maximum algal growth coincided with the period of maximum ultra-violet ray activity. Daily ('38) noted the correlation between hours of sunlight and maximum spring pulse for the phytoplankton, but he did not hold it accountable for the fall increase of plankton. Schroeder ('39) points out that the plankton includes those diatoms which grow well in abundant light, while Godward ('37) believes the occurrence of diatoms in shallow water during the winter may be due to the decrease in light penetration at that season.

Hupp ('43) states that two of the indirect results of light that may be observed are the variations in carbon dioxide and dissolved oxygen, the results of photosynthesis.

A deficiency in dissolved oxygen is thought by Pearsall ('23a) to be a limiting factor in the periodicity of certain phytoplankters (diatoms), and in another paper of the same year ('23b) he points out that most species of plankton diatoms seem to be "eu-oxybronts." In the Arctic region where the water usually has a high oxygen content, these minute plants are abundant.

Pringsheim ('46) is of the opinion that adaptation to a certain pH range need not be due to concentrations of salts outside that range interfering with protoplasmic activity, since differences in pH may also affect the solubility and therefore the availability of indispensable chemical elements such as Ca, Mg, P, and Fe.

In their study of Lake Erie, Gottschall and Jennings ('33) found that pH varied with the free carbon dioxide content and ranged from 7.6 to 8.4. Daily ('38), in his studies of Lake Michigan, noted an annual variation for hydrogen-ion concentration of from 7.4 to 8.0. He concluded that pH has little, if any, appreciable effect on seasonal periodicity of phytoplankton. However, algologists generally agree that species which make up an aquatic flora seem to be greatly influenced by pH of water, and waters of different pH have very different floras (Patrick '45).

The availability of silica is a matter of real consequence since diatoms generally constitute a large percentage of the plankton flora and this element is required by these organisms for the manufacture of their frustules (Patrick '48). Diatom periodicity is one of several factors which appears to vary with the amount of silica

present in a limnetic environment (Welsh '35, Damann '41). In 1932, Pearsall noted that diatoms failed to develop in abundance when the silica concentration was below 0.5 mg per liter. Silicon dioxide (SiO_2) in some form of soluble silicate is of common occurrence in natural waters.

Hendey ('37) believes that one of the reasons for the thin walls of tropical, aquatic diatoms is the low silica content of the water. A decrease in dissolved silica in the water following a diatom "bloom" has been frequently observed (Meloche '38, Hupp '43).

Manganese, a minor constituent of many rocks and soils, occurs in small amounts in natural waters, particularly those of acid reaction. However, apparently there is nothing in the literature even suggesting the role of this element in the nutrition of the phytoplankton. A number of investigations (Haas '32, Clark '33, Hopkins '34) indicate conclusively that manganese is an essential element for the higher chlorophyllous plants, although the amount required seems to be very small. This element is thought to play a part in oxidation and reduction phenomena, and also to be related to chlorophyll synthesis; however, its physiological effect is not yet completely understood (Meyer and Anderson '39).

Methods, Materials, and Apparatus

The quantitative study of the net phytoplankton of Quabbin Reservoir was made weekly over a period of six months, commencing on May 1, 1948 and ending on October 30, 1948. Several ecological factors were studied in conjunction with the population pulses or periodicity of the organisms, e.g., water temperature, sunlight, dissolved oxygen, carbon dioxide, hydrogen-ion concentration, soluble silicates, and manganese. A continuous record of bright sunlight and the amount of precipitation were recorded during the period of the survey.

For purposes of phytoplankton enumeration the Sedgwick-Rafter method was followed throughout (Amer. Public Health Assoc. '46). This involved (1) collection of reservoir water samples, (2) concentration by filtration, (3) examination and enumeration of the organisms, and (4) calculation of the number of phytoplankters per milliliter.

Enumeration of the net phytoplankton

A random system for the collection of samples had to be initiated because of the large area to be surveyed and the desirability of obtaining a fair representation of the phytoplankton and their environment. A grip of transparent graph-paper was placed over a map of the reservoir with the lines of the grid oriented so that one set ran directly north and south and the other set, east and west. The sides of the grid squares were each equal to 0.5 mile in length, so that each square represented an area of 0.25 square mile. Those squares which by chance happened to cover completely water areas only were arbitrarily designated as the permanent sampling stations. Islands with an area of less than 10,000 square feet were disregarded. This procedure resulted in the establishment of 36 sampling stations with no accountable land areas (fig. 1).

Triplicate samples for each of four different depths were taken from ten sampling stations once a week. These ten points were selected from the thirty-six stations with the aid of a table of random numbers (Tippett '27).

Samples were taken in the epilimnion at the surface and at depths of 2 decimeters, 4 decimeters, and 8 decimeters. These depths were arbitrarily designated in an attempt to obtain representative samples of the vertical distribution of phytoplankton of the epilimnion.

To obtain samples, three 250-ml small-mouth (inside diam. approx. 1 cm) round, glass bottles fitted with rubber stoppers were lowered in a weighted cage. When the cage with the bottles was at the desired depth the stoppers were removed by means of an attached line.

When the sample bottles had filled they were brought up and their contents transferred to 3 separate, 1-liter, Pyrex bottles. Each of the 1-liter bottles received, in turn, four 250 ml samples, one from each of the various sampling depths. The contents of two of the 1-liter bottles were studied for phytoplankton counts and the other liter of reservoir water was analyzed for the physical and chemical conditions previously mentioned.

Upon completion of a day's collection, usually around 4:00 P.M., the samples were brought into the laboratory where two of the 1-liter containers were emptied slowly through separate Sedgwick-Rafter filters. A single-hole rubber stopper fitted with a U-tube had been inserted in each of the funnel outlets, and 15 mm of 60–120 mesh filter (banding) sand placed within the funnel above the stopper. A disc of 200-mesh silk bolting cloth, having the same diameter as the inside of the funnel's outlet (12 mm), separated the sand and stopper and effectively prevented any organism or detritus with a diameter greater than 20–25 microns from being lost. Occasionally some of the filtrate was used to wash down the sides of the filters.

When the two 1-liter samples had been filtered the residuum and filter sand were washed directly into separate vials by means of 10 ml of preservative solution.[2] Thus the organisms and detritus which had been taken in the two 1-liter water samples were conveniently concentrated into two 10 ml portions of preservative solution. The vials were then corked and sealed with celloidin for future reference.

Examination and enumeration of net phytoplankton followed the procedure devised by Whipple ('27). Employing a microscope having a 16 mm objective and a 10 × ocular, the Whipple ocular micrometer was calibrated so that any observed field of the counting chamber or haemocytometer was exactly 1 sq mm.

[2] 10 parts water, 4 parts 95 per cent ethyl alcohol, 2 parts formalin (40%) and 1 part glycerine.

The residuum of a sample was loosened from the sand by swirling the vial, and transferred to the counting chamber by means of a pipette immediately after the heavier sand had settled. One ml of the preserved concentrate filled the counting chamber to capacity. The chamber was then allowed to stand for 15 minutes, to permit most of the organisms to settle to the bottom. Ten random fields, distributed more or less equidistantly over the slide, were counted for each 1 ml of concentrate in the chamber.

Inasmuch as the 1 ml of solution held in the counting chamber was a 10 to 1 concentration distributed through 1,000 fields, the number of organisms in 1 ml of reservoir water was obtained directly by totaling the number of organisms in 10 random fields. However, since the concentration did not always have the same value the following formula was useful (Amer. Public Health Assoc. '46).

$$\frac{\text{No. of fields in a 1-ml counting cell}}{\text{No. of fields counted}} \times \frac{\text{ml of concentrate}}{\text{ml of water filtered}} = \text{the multiplier}$$

"The multiplier" was the figure by which the number of organisms counted was multiplied to equal the number of organisms in 1 ml of unconcentrated reservoir water.

Three counts were made of each of the two samples, or a total of six for any collecting station, and the results averaged. Total results were computed on weekly mean counts.

Each plankter was counted as a unit regardless of the number of component cells unless it was filamentous and then it was counted once for each field it spanned. *Asterionella, Scenedesmus, Dinobryon,* and the like were considered as units. Likewise, a single cell of a colony or filament was counted as a unit if found separated from the original aggregation. Following a method used for the enumeration of blood corpuscles, cells which

touched the lower and right sides of each square were counted as if within that field.

For the quantitative portion of this paper only the genera of the organisms thus counted were tabulated and grouped into: *Myxophyceae, Euglenophyceae, Dinophyceae, Chrysophyceae, Xanthophyllaceae, Chlorophyceae, Rhodophyceae,* and *Bacillariophyceae* (*Pennales* and *Centrales*). The remainder of the samples was saved for future study in conjunction with their qualitative treatment.

Physical and chemical factors

A thermometer was placed in one of the 1-liter Pyrex jars as soon as it was filled with reservoir water and an observation in degrees Centigrade made through the container.

The number of hours of bright sunlight was recorded by means of a Raytheon photoelectric cell whose varying impulses were traced by a stylus on a cylindrical chart turned by means of a clock mechanism. Since occasional moonlight activated the photo-cell, preliminary trials indicated that it would be necessary to adjust the improvised apparatus to record only bright sunlight.

A self-contained power supply, consisting of two 6v batteries, supplied the necessary current to the apparatus for an 11- to 13-day period. For reasons of economy the recorder was checked, data noted, and fresh batteries installed only every tenth day. A new photo-cell, previously matched with the one in use, was installed on August 7, 1948 (arrow, fig. 5).

During the entire period of the survey the recorder remained in a cleared area near the water, approximately 100 yards north of Quabbin Dike (fig. 1). A rain gauge was located in the same area and recorded total precipitation for 10-day periods.

The analysis of the reservoir water for dissolved oxygen was carried out by the Winkler method (Assoc. of Official Agr. Chemists '40). A strong alkali (KOH) and potassium iodide were added to the sample along with manganous chloride. Manganous hydroxide was immediately precipitated and formed manganic hydroxide when it combined with the dissolved oxygen in the sample. A quantity of iodine, equivalent to the oxygen originally present, was then released by acidifying the solution and thus dissolving the hydroxides. The concentration of oxygen was calculated from the amount of standard solution of sodium thiosulfate used in the titration of the iodine and was given in parts per million.

The per cent of saturation of dissolved oxygen, which depends on temperature and atmospheric pressure, has also been computed. It was believed this value might be of significance since with constant atmospheric pressure the per cent of saturation decreases with a decrease in temperature even though the parts per million of dissolved oxygen remain unchanged.

Two 200-ml samples of water were tested and the results averaged. The usual precautions were taken to avoid any additional oxygen by absorption and also loss of oxygen by increase in the temperature of the sample.

Modifications of the reagents and apparatus used by Ellins and Beneker ('01) enabled the author to provide a rapid, portable test for uncombined carbon dioxide. As a result the analysis was carried out immediately after the sample had been drawn from the reservoir and errors that might have appeared if the test had been delayed were presumably avoided.

Five drops of phenolphthalein indicator solution were added to a 100- ml sample held in a Nessler tube which had its bottom painted white. The sample with indicator was titrated with 1/44N NaOH until a pink color appeared. The amount of base necessary to produce this color change, multiplied by ten, gave the amount of free carbon dioxide in ppm in the original sample.

The hydrogen-ion concentration was determined with LaMotte colorimetric ap-

paratus (Amer. Public Health Assoc. '46) at the time the sample was taken from the reservoir. Analyses were made by comparison with glass colorimetric standards and data were recorded in terms of pH.

Except for certain modifications deemed necessary, the analysis of samples for soluble silicates followed the "colorimetric-molybdate" procedure advised by the American Public Health Association ('46).

The reactions upon which this method is based are as follows: ammonium molybdate, in an acid solution of approximately pH 1.2 produces a yellow-green color with crystalloidal or non-colloidal silica if not interfered with by phosphates or tannins. Tannins did not exist in the reservoir water and the addition of oxalic acid destroyed any color contributed by phosphates.

Two ml of ammonium molybdate solution and I ml of 1 N HCl were added to 50 ml of sample in a Nessler tube. Five minutes later, 1.5 ml of oxalic acid was also added. After 30 minutes had elapsed the color of the resulting solution was compared with potassium chromate standards.

The standards were prepared as follows: 0.63 g of K_2CrO_4 were dissolved in a liter of distilled water and volumes of from 1 ml to 10 ml, respectively, were diluted with 25 ml of a 1 per cent solution of sodium tetraborate and enough distilled water to make 55 ml of solution. The silica in parts per million for the sample compared was then determined by multiplying by two the ml of potassium chromate solution in the standard.

Investigations conducted by the writer prior to the present survey indicated a complete lack of manganese in the epilimnion region. Furthermore, Reed('47) concluded from his study of the character of Quabbin water that manganese has not appeared above the 50-ft level since 1944. In view of this, the use of a non-quantitative test merely to determine the presence or absence of manganese was considered justifiable.

In all cases, the data obtained (numbers of net phytoplankton and physical and chemical conditions) from each of the ten random sampling stations for any one week were averaged and accepted as the mean for that particular period.

Results

Quantitative collections of the net phytoplankton of Quabbin Reservoir which were taken from May 6, 1948 to October 30, 1948 yielded 68 genera representing 7 classes of algae.[3] *Bacillariophyceae* (diatoms) averaged 79.5% of the total yield, dominating all but four of the collections. *Myxophyceae* was the most abundant class in these four samples collected on consecutive weeks from August 26 to September 16 and accounted for 14.1% of the total yield of the study. *Chlorophyceae* and *Chrysophyceae* were present in all but a single sample and averaged 5.4% and 1.2%, respectively, of the total net phytoplankton. The *Dinophyceae, Xanthophyceae*, and *Euglenophyceae* were absent from a majority of the samples; each of these classes accounted for less and 0.1% of the total yield for the six months period. The complete data on the occurrence of the various classes of net phytoplankton are given in table I.

Four definite pulses or sudden population increases were observed for the organisms studied. These occurred with diminishing severity on June 17, July 29, September 9, and October 7 (fig. 2). *Myxophyceae* were responsible for the increase of September 9, while diatoms were accountable for the other peaks. The curve for diatoms conforms with that of total net phytoplankton except during the "blue-green" pulse.

The greatest weekly change in yield oc-

[3] Only those organisms which were collected at more than one sampling station on the same day are included in the quantitative portion of this paper.

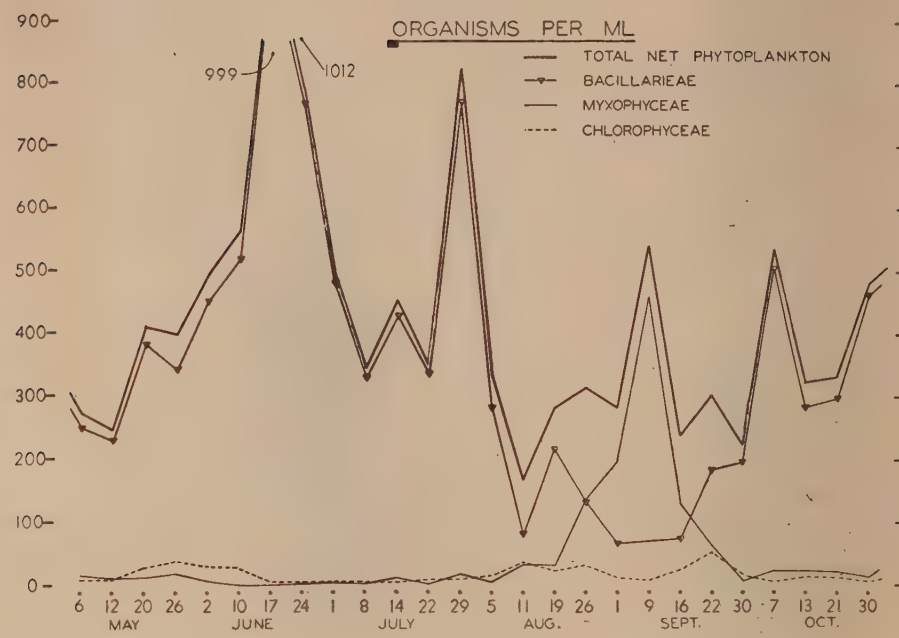

FIG. 2. Organisms (net phytoplankton) per milliter. (*Bacillarieae* are referred to as *Bacillariophyceae* in the text.)

curred prior to the first pulse (June 17) when the net phytoplankton increased from 562.5 to 1,012.5 per ml. The minimum yield of 166 per ml was obtained on August 11. It is interesting to note that this was also the only collection taken during the period from July 14 to October 30 in which *Chlorophyceae* were more numerous than *Myxophyceae*. The relationships existing between the periodic-

TABLE I. *Net phytoplankton: weekly averages expressed in numbers per ml and per cent of the total yield*

	May				June				July					
	6	12	20	26	2	10	17	24	1	8	14	22	29	
Bacillariophyceae:														
Pennales:	209	153.5	320.5	281	395.5	494	972.5	766	479.5	319	395	323	770	Per ml
Centrales:	38	74	60.5	59	59.5	27	26.5	12.5	2.5	13.5	33	12.5	1.5	Per ml
Totals:	247	227.5	381	340	455	521	999	778.5	482	332.5	428	335.5	771.5	Per ml
	90.9	92.5	90.6	85.8	91.9	92.7	98.7	98.8	97.2	96.5	94.3	95.4	94	Per cent
Myxophyceae:	15	10	11.5	18	6.5	1.5	1.5	2.5	4.5	4	13.5	3.5	18	Per ml
	5.5	4.1	2.7	4.5	1.3	0.3	0.2	0.3	0.9	1.2	3	1	2.2	Per cent
Chlorophyceae:	9	7	26.5	36.5	30	28	7	6	7.5	6.5	7	10	10.5	Per ml
	3.3	2.8	6.3	9.2	6.1	5.0	0.7	0.8	1.5	1.9	1.5	2.8	1.3	Per cent
Chrysophyceae:	0.5	1.5	1.5	1.5	3	11	4.5	0	1.5	1.5	4.5	2.5	19.5	Per ml
	0.2	0.6	0.4	0.7	0.6	2	0.4	0	0.3	0.4	1.0	0.8	2.4	Per cent
*Dinophyceae:**	0	0	0	0.5	0	0	0	0	0.5	0	0	0	0.5	Per ml
*Xanthophyceae:**	0	0	0	0	0.5	0.5	0.5	1	0.5	0	1.0	0	0	Per ml
*Euglenophyceae:**	0	0	0	0	0	0.5	0	0	0	0	0	0	0.5	Per ml
Weekly totals:	271.5	246	420.5	396.5	495	562.5	1012.5	788	496.5	344.5	454	351.5	820.5	Per ml

* Percentages for these classes not computed

TABLE I—*Continued*

	August				September					October				
	5	11	19	26	1	9	16	22	30	7	13	21	30	
Bacillariophyceae:														
Pennales:	269	50	187	54.5	41.5	31.5	69.5	139	181.5	456	331.5	257	375	Per ml
Centrales:	14	31.5	35.5	79.5	24	39.5	15	45	14.5	48.5	52	40.5	89	Per ml
Totals:	283	81.5	217.5	134	65.5	71	74.5	184	196	504.5	283.5	297.5	464	Per ml
	84.1	49.1	77	42.6	23.2	13.1	31.1	60.5	87.5	94.3	87.8	89.9	95.9	Per cent
Myxophyceae:	6	32.5	31	136.5	197.5	457.5	139	64	6.5	23.5	23.5	20.5	13.5	Per ml
	1.8	19.6	11	43.4	70	84.5	58	21.1	2.9	4.4	7.3	6.2	2.8	Per cent
Chlorophyceae:	16	37.5	24	32.5	12.5	8	25	52	16.5	6	13	12.5	5.5	Per ml
	4.8	22.6	8.5	10.3	4.4	1.5	10.4	17.1	7.4	1.1	4.0	3.8	1.1	Per cent
Chrysophyceae:	31.5	13	9	7.5	6	3.5	1	4	4.5	0.5	1.5	0.5	0.5	Per ml
	9.4	4.0	3.2	2.4	2.1	0.6	0.4	1.3	2.0	0.1	0.4	0.2	0.1	Per cent
*Dinophyceae:**	0	1.0	0.5	3.5	0	0.5	0	0	0.5	0.5	0.5	0	0.5	Per ml
*Xanthophyceae:**	0	0.5	0.5	0	0	0.5	0	0	0	0	0.5	0	0	Per ml
*Euglenophyceae:**	0	0	0	0.5	0.5	0	0	0	0	0	0.5	0	0	Per ml
Weekly totals:	336.5	166	282.5	314.5	282	541	239.5	304	224	535	323	331	484	Per ml

ity of the net phytoplankton and some of their environmental conditions are indicated in figure 4 while these physical and chemical factors are summarized in table V.

Net phytoplankton abundance

The ubiquitous diatoms were the most abundant class of phytoplankton in Quabbin Reservoir averaging slightly over 350 per ml in the epilimnion (fig. 2) and accounting for 79.5% of the total yield for the survey (table I). The greatest concentration was evident on June 24 when 98.8% of the phytoplankton was comprised of *Bacillariophyceae* while 13.1% was the lowest record attributed to this class (fig. 3). The low occurred on Sep-

TABLE II. *Bacillariophyceae: weekly averages expressed in numbers per ml*

	May				June				July				
	6	12	20	26	2	10	17	24	1	8	14	22	29
Pennales:													
Tabellaria	23	12	19	37	26	22	12	32	53	38	114	136	615
Diatoma	2	p	—	1	2	p	p	—	1	2	p	—	—
Fragilaria	18	3	p	2	5	6	5	12	21	63	177	104	63
Synedra	15	12	34	23	82	19	36	205	287	168	83	20	31
Asterionella	71	88	236	197	231	419	887	505	99	22	13	48	50
Navicula	9	p	5	p	5	4	p	1	5	17	3	p	6
Pinnularia	1	p	p	1	p	1	1	4	p	1	—	3	2
Pleurosigma	1	p	—	—	—	—	—	—	—	—	—	—	—
Amphiprora	p	—	—	p	1	5	p	p	p	1	2	p	—
Gomphonema	p	p	—	7	—	p	—	—	—	—	—	—	—
Cymbella	29	12	p	—	p	—	9	p	—	—	—	—	—
Nitzschia	37	23	21	9	38	13	19	3	12	5	2	10	3
Cymatopleura	2	1	4	1	4	3	2	3	p	2	p	1	—
Surirella	—	—	—	2	p	1	—	—	—	—	—	—	—
Sub-totals:	209	153.5	320.5	281	395.5	494	972.5	766	479.5	319	395	323	770
Centrales:													
Melosira	19	64	33	24	31	23	16	3	—	—	p	—	—
Cyclotella	17	6	9	29	19	2	p	3	p	10	32	12	p
Stephanodiscus	—	3	18	4	9	1	9	p	—	3	p	—	—
Rhizosolenia	2	1	p	2	p	1	1	6	2	p	—	p	1
Sub-totals:	38	74	60.5	59	59.5	27	26.5	12.5	2.5	13.5	33	12.5	1.5
Totals	247	227.5	381	340	455	521	999	778.5	482	332.5	428	335.5	771.5

p = Organism present at two or more sampling stations but not in sufficient quantity to equal 1 per ml; for purposes of calculation, p equals 0.5 per ml

TABLE II—*Continued*

	August				September					October			
	5	11	19	26	1	9	16	22	30	2	13	21	30
Pennales:													
Tabellaria	198	26	39	3	17	7	29	58	31	105	32	55	173
Diatoma	—	p	—	—	—	—	—	—	1	—	p	—	—
Fragilaria	13	p	5	p	—	2	11	p	9	13	4	19	29
Synedra	9	12	65	32	17	11	7	49	42	30	8	21	63
Asterionella	45	4	24	6	3	p	3	8	85	299	181	153	88
Navicula	p	2	22	7	p	9	1	4	p	3	p	p	1
Pinnularia	p	—	—	—	—	—	p	1	p	2	1	5	4
Pleurosigma	—	—	—	—	—	—	—	—	—	—	—	—	p
Amphiprora	—	p	2	p	1	—	1	p	—	—	—	—	—
Gomphonema	p	—	4	—	—	—	—	—	—	—	p	p	—
Cymbella	—	p	—	—	p	p	9	17	12	3	1	p	6
Nitzschia	2	4	21	5	p	p	4	p	—	—	1	2	9
Cymatopleura	p	—	—	p	2	1	4	p	p	1	2	p	p
Surirella	—	—	—	—	—	—	—	—	—	—	—	—	—
Sub-totals:	269	50	187	54.5	41.5	31.5	69.5	139	181.5	456	231.5	257	375
Centrales:													
Melosira	4	8	22	1	p	—	p	41	13	37	50	31	73
Cyclotella	6	19	13	78	23	39	14	3	p	5	1	p	2
Stephanodiscus	—	p	—	—	—	—	—	—	p	6	p	9	14
Rhizosolenia	4	4	p	p	p	p	p	1	p	p	p	—	—
Sub-totals:	14	31.5	35.5	79.5	24	39.5	15	45	14.5	48.5	52	40.5	89
Totals	283	81.5	217.5	134	65.5	71	74.5	184	196	504.5	283.5	297.5	464

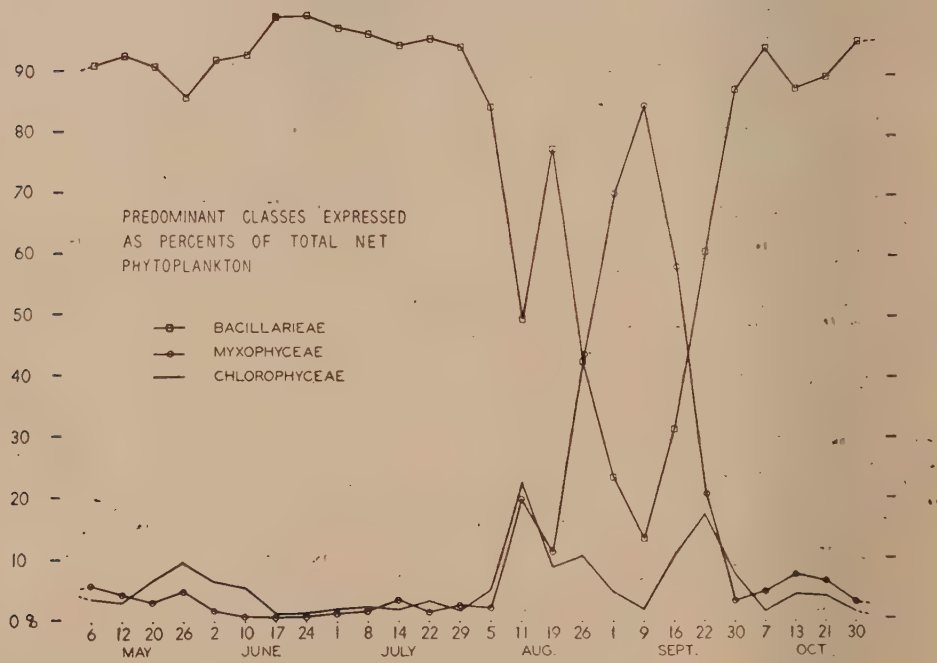

FIG. 3. Predominant classes of net phytoplankton expressed as per cents of total.

tember 9 when *Myxophyceae* were at their maximum. Numerically, diatoms were at their ebb during the previous week (table I).

Twenty-two genera of *Bacillariophyceae* were noted. Eighteen of these genera belonged to the order *Pennales,* and the remaining four were members of the *Cen-*

trales (table II). The centric types were responsible for only 10% of the diatoms and were more numerous than the pendant forms in only two collections, those of August 26 and September 9.

At least one distinct pulse was found each month from May to October among the various genera of diatoms (table II). These peaks of abundance occurred in the following order: *Melosira* in May, though *Asterionella* which followed in June was then numerically greater; *Synedra* in early July, *Fragillaria* and *Tabellaria* in late July, *Cyclotella* in August, minor pulses of *Melosira* and *Synedra* in September, and *Asterionella, Tabellaria,* and *Melosira* repeating in October. The pendant forms generally exhibited their maximum development in spring while the centric forms were more abundant in the fall.

Asterionella and *Tabellaria* were the numerically dominant diatoms, followed by *Synedra* and *Fragellaria. Nitzschia* and *Navicula* of the *Pennales, and Melosira* and *Cyclotella* of the centric types were frequently abundant but never dominated the samples. The remainder of the *Bacillariophyceae* (table II) were found sporadically in sparse numbers, many of them being merely facultative plankton.

The *Myxophyceae* which averaged 14.2% of the total yield for this study appear to have a single period of abundance

TABLE III. Chlorophyceae: *weekly averages expressed in numbers per ml*

	May				June				July				
	6	12	20	26	2	10	17	24	1	8	14	22	29
Chlamydomonas	—	—	—	—	—	—	—	p	p	p	—	—	—
Gonium	6	1	5	p	1	p	1	1	—	—	p	—	p
Pandorina	2	p	10	19	3	7	p	2	p	—	—	—	p
Eudorina	—	p	8	1	5	11	3	p	1	1	—	—	p
Volvox	—	—	—	—	—	—	p	—	p	p	1	—	—
Sphaerocystis	—	p	—	—	p	p	—	—	p	1	—	p	p
Asterococcus	—	—	—	p	—	—	—	—	—	—	—	—	—
Tetraspora	—	—	—	—	p	—	—	—	—	—	—	—	—
Pediastrum	—	—	p	—	1	—	p	p	2	1	—	p	—
Coelastrum	—	p	—	—	p	p	—	—	p	—	—	p	—
Dictyosphaerium	—	—	—	—	p	p	—	—	—	p	p	7	2
Oocystis	—	—	—	p	—	p	—	—	—	—	—	p	1
Lagerheimia	—	—	—	—	—	—	—	—	p	—	—	—	—
Dimorphococcus	—	—	—	—	—	p	—	—	—	—	—	p	—
Selenastrum	—	p	p	p	—	—	—	—	—	—	—	—	—
Quadrigula	—	—	—	—	—	p	—	—	—	—	—	—	—
Kirchneriella	—	—	p	—	—	—	—	p	p	p	—	—	—
Tetraedron	—	p	—	—	—	p	1	—	p	—	—	—	p
Scenedesmus	p	p	—	p	p	—	1	p	—	p	—	—	2
Actinastrum	—	—	—	—	p	—	—	—	—	—	p	p	—
Micratinium	—	—	—	—	—	—	—	—	—	p	—	—	—
Spirogyra	—	—	—	p	—	—	—	—	—	—	p	—	—
Netrium	—	—	—	—	—	—	—	—	—	—	—	—	—
Closterium	—	—	p	—	p	—	—	—	—	—	p	—	—
Pleurotaenium	—	—	—	—	—	p	—	—	—	—	—	—	—
Cosmarium	—	—	p	p	—	—	—	—	p	—	—	—	—
Cosmocladium	—	—	—	—	—	—	—	—	—	—	p	—	—
Xanthidium	—	—	—	—	—	—	p	—	—	—	—	—	—
Staurastrum	—	2	—	10	p	—	—	—	—	p	3	—	p
Sphaerozosma	p	—	p	3	16	5	—	p	—	—	—	—	2
Hyalotheca	—	p	—	—	—	p	—	—	—	—	—	—	—
Totals	9	7	26.5	36.5	30	28	7	6	7.5	6.5	7	10	10.5

p = Organism present at two or more sampling stations but not in sufficient quantity to equal 1 per ml; for purposes of calculation, p equals 0.5 per ml

TABLE III—*Continued*

	August				September					October			
	5	11	19	26	1	9	16	22	30	7	13	21	30
Chlamydomonas	p	1	2	p	p	—	p	p	—	—	—	—	—
Gonium	p	—	—	p	p	p	—	—	—	—	1	p	—
Pandorina	—	—	p	p	—	1	11	2	8	3	p	1	1
Eudorina	—	p	—	—	—	2	p	8	1	—	1	—	p
Volvox	—	p	p	p	2	p	—	—	—	—	—	—	—
Sphaerocystis	9	2	1	—	p	p	—	p	—	—	—	p	p
Asterococcus	—	—	—	—	—	—	—	—	—	p	—	—	—
Tetraspora	—	—	p	—	—	—	—	—	—	—	—	—	—
Pediastrum	—	3	5	2	p	1	—	p	—	—	—	1	p
Coelastrum	p	1	—	—	p	—	—	—	p	p	—	—	—
Dictyosphaerium	—	p	—	p	—	—	p	2	—	—	—	p	—
Oocystis	—	—	—	—	—	p	p	p	—	—	—	—	—
Lagerheimia	—	—	—	—	—	—	p	—	—	—	—	—	—
Dimorphococcus	—	—	p	p	—	p	—	p	—	—	—	—	—
Selenastrum	—	—	—	—	—	—	—	p	—	p	p	—	p
Quadrigula	—	—	—	—	—	—	—	p	—	—	—	—	—
Kirchneriella	p	—	—	—	—	p	—	—	—	—	—	p	—
Tetraedron	—	1	3	p	1	—	—	4	—	p	p	1	p
Scenedesmus	3	26	8	p	p	—	1	p	p	—	p	2	—
Actinastrum	—	—	—	—	—	p	—	p	—	—	—	—	—
Micratinium	p	—	—	—	—	—	—	—	—	—	—	—	—
Spirogyra	—	p	—	—	—	—	—	—	—	—	—	—	p
Netrium	—	—	p	—	—	—	p	—	—	—	—	—	—
Closterium	—	—	1	2	p	—	—	p	1	—	—	p	p
Pleurotaenium	—	—	p	—	—	—	—	—	—	—	—	p	—
Cosmarium	p	p	—	—	—	—	p	—	1	p	—	p	—
Cosmocladium	p	p	—	—	—	—	—	—	—	—	—	—	—
Xanthidium	—	p	—	—	—	—	—	p	—		p	—	—
Staurastrum	—	—	p	23	5	—	p	27	4	—	8	3	p
Sphaerozosma	p	—	p	1	1	p	9	3	p	p	p	—	p
Hyalotheca	—	—	—	—	—	—	—	p	—	—	—	—	—
Totals	16	37.5	24	32	12.5	8	25	52	16.5	6	13	12.5	5.5

(fig. 2). This definite pulse dominated all other organisms from August 26 to September 16 and reached its maximum amplitude on September 9 when *Myxophyceae* accounted for 84.5% of the total phytoplankton (fig. 3). It is also significant that *Anabaena* was responsible for 93% of the blue-greens taken in this collection (table IV). The lowest record for the class occurred during the time of the strongest diatom pulse, June 10 to 17, when only 1.5 per ml or 0.2% of the total net phytoplankton was identified as *Myxophyceae* (fig. 3, table I).

Of the ten genera collected, the order *Hormogonales,* represented by *Oscillatoria, Lyngbya, Anabaena, Aphanizomenon* and *Gloeotrichia,* was the outstanding group of the class, with *Anabaena* the dominant form. The *Chroococcales,* represented mainly by *Microcystis* and *Merismopedia,* were frequently present but never abundant.

Chlorophyceae were represented by 31 genera (table III), the outstanding ones being *Pandorina* and *Eudorina* of the order *Volvocales, Sphaerocystis* of the *Tetrasporales, Scenedesmus* of the *Chlorococcales,* and *Staurastrum* and *Sphaerozosma* of the *Zygnematales.* The other genera were of infrequent occurrence.

The green algae were never very numerous but were present in every collection and yielded an average of 5.4% of the total organisms studied (table I). There were no distinct pulses observed as with the two previous classes; however, population increases of diatoms and blue-greens seem to have an inverse effect on *Chlorophyceae* since the minima recorded

for the greens coincide with the maxima of *Bacillariophyceae* and *Myxophyceae* (fig. 4). The *Chlorophycean* pulses occurred in May, August and September. On August 11, 22.6% of the total yield was attributed to this class (table III).

Only four genera of *Chrysophyceae,* all members of the order *Chrysomonadales,* were observed during this study. This class was never abundant and accounted for only 1.2% of the total net phytoplankton (table I). Yet, during the week of August 5, at the time of their only population pulse, the *Chrysophyceae,* represented mainly by *Synura* (table IV), outnumbered the combined *Chlorophyceae* and *Myxophyceae* and constituted 9.4% of the yield. *Dinobryon* and *Mallomonas* were present in a majority of collections, while *Uroglenopsis* was present in but two quantitative samples, those of August 11 and September 1 (table IV).

Since only 40% of the weekly samples contained *Dinophyceae* and less than 1% of the organisms enumerated were members of this class, no significant trends could be ascertained (table I). The two genera observed were *Ceratium* and *Peridinium. Ceratium* was present to the extent of 3 organisms per ml on August 20 while *Peridinium* was exceedingly rare (table IV).

Botryococcus and *Ophiocytium* represented the scarce and sporadic class *Xanthophyceae.* The highest concentration of this class appeared on July 24 when *Botryococcus* reached a population level of one organism per ml. *Ophiocytium* was collected in quantity only twice, once during July and again in August (table IV).

Phacus was the singular representative of the class *Euglenophyceae.* This genus was recorded once for each month from June through October (table IV). Other members of this class were present but only the chlorophyllous forms were enumerated.

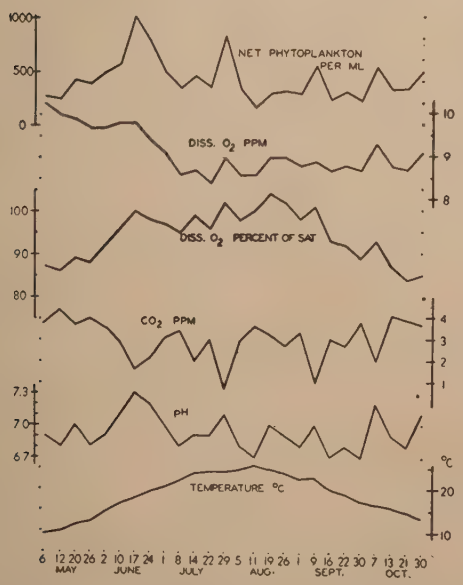

FIG. 4. Graphs showing correlations between total net phytoplankton and a few environmental factors.

Relation of physical and chemical conditions to populations

The highest temperature recorded for the epilimnion of Quabbin Reservoir was 25.3° C which was reached on August 11. The lowest temperature, 9.3° C, was observed on the first day of the survey, May 6 (table V, fig. 4). A maximum weekly increase in temperature took place between May 26 and June 2 when the temperature of the water rose from 12.1° C to 14.3° C, a range of 2.2° C. However, the greatest weekly change was exhibited from September 9 through September 16 when the temperature fell 2.4° C (table V). At the close of the study the water temperature was 13.3° C.

The abundance of net phytoplankton in the first few months of the survey seemed to follow, to a degree, the steady rise in temperature of the epilimnion (fig. 4). The October increase in phytoplankton, however, took place when the temperature was steadily declining. No major pulse was evident at the time of the highest temperature; in fact, the lowest record for total net phytoplankton was obtained

on this date. A marked population increase did occur for *Tabellaria* two weeks previous to the highest recorded temperature. At this time the temperature of the water was 23.8° C (table V).

Classes *Myxophyceae, Chrysophyceae,* and to a lesser extent *Dinophyceae* had their maximum development when the temperature of their environment was above 20° C. *Volvocales* (*Chlorophyceae*) appear to grow best in the cooler waters of spring and fall. Abundance of a few isolated genera (*Synura, Scenedesmus, Microcystis*) of other classes was also positively correlated with the temperature curve.

Considering only the mean for ten-day periods, hours of bright sunshine varied from 2.7 hours to 9.9 hours per day (fig. 5). The period of May 10 through May 20 provided the minimum mean record, while the maximum average was made June 29 through July 8. The lowest monthly average for hours of bright sunshine was observed during October when a mean of 4.0 hours was registered. An average of over 9.5 hours of sunshine was noted for July giving this month the highest mean of the survey (table V).

The hours of bright sunshine appear to have an important correlation with the July maxima of some of the phytoplank-

TABLE IV. Myxophyceae, Xanthophyceae, Chrysophyceae, Dinophyceae, Euglenophyceae: *weekly averages expressed in numbers per ml*

	May				June				July				
	6	12	20	26	2	10	17	24	1	8	14	22	29
Myxophyceae:													
Chroococcus	—	—	—	—	—	—	—	—	—	—	—	—	—
Microcystis	—	—	—	—	p	—	—	p	3	—	—	p	5
Merismopedia	13	2	10	p	2	—	p	p	—	—	—	—	—
Coelosphaerium	—	—	p	p	—	—	p	—	p	1	—	p	—
Gomphosphaeria	—	—	—	—	—	—	—	—	—	—	—	—	—
Oscillatoria	—	—	—	p	—	p	—	p	p	—	1	p	—
Lyngbya	—	1	—	p	p	—	—	1	—	p	p	—	p
Anabaena	2	7	1	16	3	1	p	—	p	2	13	1	12
Aphanizomenon	—	—	—	—	p	—	—	—	—	p	—	1	p
Gloeotrichia	—	—	—	—	—	—	—	—	—	—	—	—	—
Totals:	15	10	11.5	18	6.5	1.5	1.5	2.5	4.5	4	13.5	3.5	18
Xanthophyceae:													
Botryococcus	—	—	—	—	p	p	p	1	p	—	p	—	—
Ophiocytium	—	—	—	—	—	—	—	—	—	—	p	—	—
Totals:	0	0	0	0	0.5	0.5	0.5	1	0.5	0	1	0	0
Chrysophyceae:													
Mallomonas	—	p	p	p	1	10	3	—	p	—	p	—	p
Synura	p	—	p	—	2	p	1	—	p	p	3	p	5
Uroglenopsis	—	—	—	—	—	—	—	—	—	—	—	—	—
Dinobryon	—	1	p	1	—	p	p	—	p	1	1	2	14
Totals:	.5	1.5	1.5	1.5	3	11	4.5	0	1.5	1.5	4.5	2.5	19.5
Dinophyceae:													
Peridinium	—	—	—	—	—	—	—	—	—	—	—	—	—
Ceratium	—	—	—	p	—	—	—	—	p	—	—	—	p
Totals:	0	0	0	.5	0	0	0	0	0.5	0	0	0	0.5
Euglenophyceae:													
Phacus	—	—	—	—	—	p	—	—	—	—	—	—	p

p = Organism present at two or more sampling stations but not in sufficient quantity to equal 1 per ml. For purposes of calculation, p equals 0.5 per ml

TABLE IV—*Continued*

	August				September					October			
	5	11	19	26	1	9	16	22	30	7	13	21	30
Myxophyceae:													
Chroococcus	—	—	p	—	p	—	—	—	—	p	p	—	—
Microcystis	p	9	20	82	16	23	13	42	p	4	p	1	—
Merismopedia	—	p	p	3	—	—	—	2	p	1	19	18	2
Coelosphaerium	1	p	p	1	9	2	p	1	1	—	p	—	—
Gomphosphaeria	—	p	—	—	—	—	p	—	—	—	—	—	—
Oscillatoria	p	—	2	p	p	—	p	—	—	p	—	—	p
Lyngbya	—	p	3	p	1	p	p	3	p	—	—	p	—
Anabaena	4	21	3	49	158	430	81	9	3	17	2	p	11
Aphanizomenon	—	p	1	p	13	2	43	7	p	—	1	p	—
Gloeotrichia	—	—	p	—	—	—	—	—	p	—	—	—	—
Totals:	6	32.5	31	136.5	197.5	457.5	139	64	6.5	23.5	23.5	20.5	13.5
Xanthophyceae:													
Botryococcus	—	—	p	—	—	p	—	—	—	—	p	—	—
Ophiocytium	—	p	—	—	—	—	—	—	—	—	—	—	—
Totals:	0	0.5	0.5	0	0	0.5	0	0	0	0	0.5	0	0
Chrysophyceae:													
Mallomonas	p	—	—	—	p	—	p	3	p	—	p	—	—
Synura	27	12	4	7	1	3	p	p	3	p	—	—	p
Uroglenopsis	—	p	—	—	p	—	—	—	—	—	—	—	—
Dinobryon	4	p	5	p	4	p	—	p	1	—	1	p	—
Totals:	31.5	13	9	7.5	6	3.5	1	4	4.5	0.5	1.5	0.5	0.5
Dinophyceae:													
Peridinium	—	p	—	p	—	—	—	—	—	—	p	—	—
Ceratium	—	p	p	3	—	p	—	—	p	p	—	—	p
Totals:	0	1	0.5	3.5	0	0.5	0	0	0.5	0.5	0.5	0	0.5
Euglenophyceae:													
Phacus	—	—	—	p	p	—	—	—	—	—	p	—	—

ton, notably: *Synedra, Fragillaria* and *Tabellaria* of the *Bacillariophyceae; Dinobryon* of the *Chrysophyceae;* and *Dictyosphaerium* of the *Chlorophyceae.* Yet there are obvious discrepancies in any attempted correlation between visible solar radiation and total net phytoplankton yield (figs. 2, 5). Important as sunlight is for the optimum growth of all chlorophyllous plants it does not seem to be the controlling factor in phytoplankton periodicity.

A range of only 1.8 ppm for dissolved oxygen in the epilimnion was found. The highest concentration, 10.2 ppm, occurred on May 6, and the lowest, 8.4 ppm, was found on July 22 (table V).

An increase in temperature normally decreases the solubility of oxygen in water. Thus saturation of a given quantity of warmer water is reached with less oxygen than in the same amount of colder water. Therefore, the recordings for dissolved oxygen in percentages of saturation are more representative of the prevailing physical conditions than are those which express dissolved oxygen in units per volume.

The curves depicting temperature and per cent of saturation of the dissolved oxygen parallel each other except during phytoplankton pulses (fig. 4). Fluctuations in per cent of saturation were the results of increased oxygen from photosynthetic activity. By plotting weekly results (table V) a remarkably close posi-

tive correlation is manifest between total yield of algae and dissolved oxygen (fig. 4).

Dissolved oxygen, varying as it does with relative abundance of net phytoplankton, appears to be a limiting factor. These correlative variations are misleading since a large percentage of dissolved oxygen is due to the presence of chlorophyllous plankton which evolve O_2 during the day and utilize it in respiration during times of darkness.

Since all samples were collected during the day, free carbon dioxide of the water was found to be inversely related to the amount of net phytoplankton present. As with any gas the amount of CO_2 retained by water depends to a considerable extent on temperature. The epilimnion of Quabbin Reservoir exhibited a range for free carbon dioxide of 3.7 ppm (fig. 4). The lowest concentration of CO_2, 0.7 ppm, was detected on July 29 (table V) when the temperature of the water was slightly less than 24° C and the phytoplankton were at their second highest concentration (820.5 per ml). On May 12 the water held the maximum amount of free CO_2 (4.4 ppm) of the study. At this time the water temperature was only 9.9° C and

TABLE V. *Physical and chemical conditions*

	Date of sample	Temperature °C	Diss. O_2 ppm	Diss. O_2 – % of saturation	Free CO_2 ppm	pH	SiO_2 ppm
May	6	9.3	10.2	87	3.8	6.9	9.3
	12	9.9	10.0	86	3.4	6.8	10.5
	20	11.4	9.9	89	3.7	7.0	13.4
	26	12.1	9.7	88	4.0	6.8	15.2
June	2	14.3	9.7	92	3.5	6.9	11.9
	10	16.1	9.8	96	2.9	7.1	3.6
	17	17.6	9.8	100	1.6	7.3	8.3
	24	19.1	9.4	98	2.1	7.2	10.0
July	1	20.2	9.1	97	3.1	7.0	10.4
	8	21.7	8.6	95	3.4	6.8	8.1
	14	23.5	8.7	99	2.0	6.9	12.0
	22	23.9	8.4	96	3.0	6.9	4.4
	29	23.8	9.0	102	0.7	7.1	7.0
August	5	24.4	8.6	98	2.9	6.8	8.1
	11	25.3	8.6	100	3.6	6.7	5.9
	19	24.5	9.0	104	3.2	7.0	10.1
	26	23.6	9.0	102	2.7	6.9	9.7
September	1	22.3	8.8	98	3.3	6.8	12.0
	9	22.4	8.9	101	1.0	7.0	10.5
	16	20.0	8.7	93	3.0	6.7	12.3
	22	18.8	8.8	92	2.7	6.8	9.8
	30	17.1	8.7	89	3.8	6.7	3.9
October	7	16.4	9.3	93	2.0	7.2	7.6
	13	15.9	8.8	87	4.1	6.9	8.2
	21	14.8	8.7	84	3.9	6.8	5.9
	30	13.3	9.1	85	3.7	7.1	4.3

Hours of Sunshine
(Daily averages for 10-day periods)

May			June			July			August			September			October		
10	20	30	9	19	29	8	18	28	7	17	27	6	16	26	6	16	26
7.9	2.7	2.8	5.0	5.1	7.1	9.9	9.3	9.5	7.6	4.9	8.0	6.9	8.3	6.4	6.0	3.3	2.8

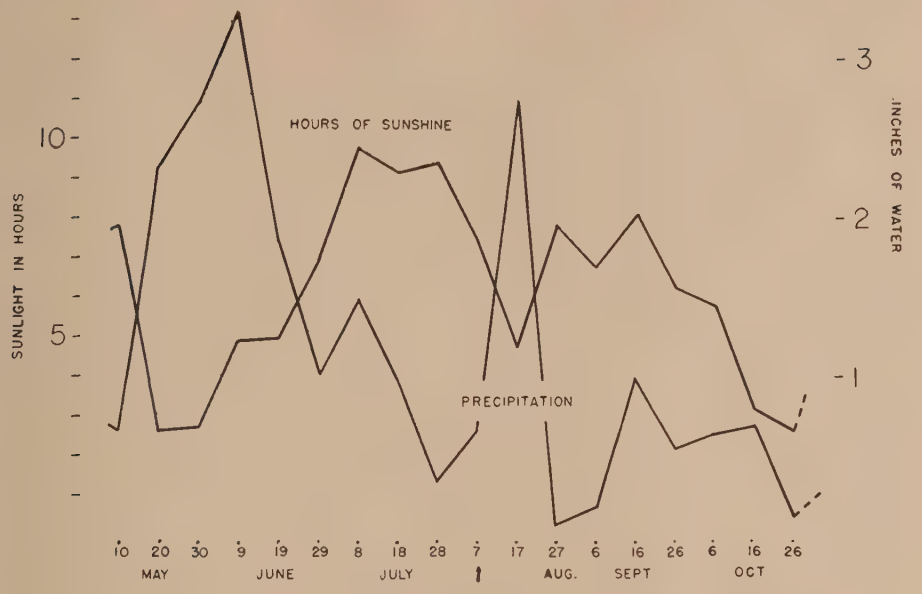

FIG. 5. Hours of sunshine and inches of precipitation.

the total phytoplankton curve demonstrated one of its first depressions (fig. 4).

As indicated in figure 6 the curve for CO_2 and the curves for pH and dissolved oxygen are almost inversely proportional. Fluctuations in amount of CO_2 appear to be caused by reduction of photosynthesis.

The hydrogen-ion concentration of the circumneutral water of the reservoir showed a very restricted range. On August 11 and on September 16 and again on September 30 the pH was observed to be 6.7. These readings were the lowest of the study and in each instance the net phytoplankton population was at a very low ebb (fig. 4). The highest pH, 7.3, was recorded on June 17 and this peak coincided with the largest population pulse of the study.

As an inverse proportionality is strongly suggested (fig. 4), the abundance of chlorophyllous plankton appears to be limited by the hydrogen-ion cencentration of the environment. However, comparisons with CO_2 data (table V) indicate that fluctuations in pH might be caused by varying concentrations of algae on the basis of CO_2 utilization in photosynthesis.

Development of *Chlorophyceae* seemed to be retarded by a low hydrogen-ion concentration as all their population increases occurred in slightly acid water. The apparent preference for a relatively low pH by this class may be actually the manifestation of a high CO_2 demand.

Silicates varied from a low of 3.6 ppm to a high of 15.2 ppm (table V). Two factors were found to contribute to the concentration of silicates. Precipitation caused increases in silicates by adding to the flow of the tributaries, and diatom pulses decreased the silicates by the utilization of silicon for construction of frustules.

The most pronounced increase in silicates came during the week of August 12 through August 19 when an increase of 4.2 ppm was noted (table V). On the second and third day of this week precipitation amounted to 2.8 inches of water and accounted for 75 per cent of the total rainfall for the month of August (fig. 5).

There existed a correlation between soluble silicates and diatom periodicity in that silicates decreased suddenly prior to increases in population of *Bacillariophy-*

FIG. 6. Bacillariophyceae and silica yields compared.

ceae (fig. 6). The availability of soluble silicates may be a factor in limiting the amplitude of diatom pulses but it seems to exert little effect upon the periodicity of the total net phytoplankton.

Tests for manganese demonstrated a complete lack of this element in the epilimnion.

DISCUSSION

Considering only the four major pulses, the two spring and the single fall amplitudes in total net phytoplankton were the result of increases in *Bacillariophyceae* while the late summer peak was caused by a rise in *Myxophyceae*. These two classes accounted for nearly 94% of the total phytoplankton; the *Bacillariophyceae* alone amounted to 79.6% of the yield. These figures compare favorably with the findings of Daily ('38) and Damann ('41) for Lake Michigan and Gottshall and Jennings ('33) for Lake Erie. These investigators also found peaks of abundance of the dominant genera of diatoms to be in the same order as found in Quabbin Reservoir. This succession commencing with *Asterionella* is believed by Pearsall ('32) to be due to the higher nutritive requirements of this form over the succeeding genera. Akehurst ('31), however, believes that the succession is due to the fact that one group produces substances which are toxic to itself but stimulating to another. In other words, *Asterionella* may exude a substance toxic to itself but stimulating, in this case, to *Synedra*.

As noted by Chandler ('40) those genera of *Bacillariophyceae* which are at their greatest development in the spring belong to the *Pennales*, while the *Centrales* include many forms which are most abundant in the fall.

The autumnal maximum of blue-greens of Quabbin is consistent with the results of similar investigations as undertaken by the Wests ('12), Tiffany ('34), and others.

Myxophyceae have been reported to be sparse in lakes that have very pure water (West and West '12). White ('31) is of the opinion that their numbers are determined by the amount of nitrogenous matter in the water. Results of this study indicate that several factors contribute to abundance of *Myxophyceae*, and tempera-

ture is apparently one of the more important of these conditions. The predominance of *Hormogonales* with *Anabaena* as the dominant form is similar to what Daily ('38) found in his studies of Lake Michigan.

Reasonable conclusions concerning seasonal growth of the *Chlorophyceae* are difficult to make in view of the low yield. However, the periods of amplitude for this class occurred in times of low pH and thus of relatively high concentrations of free carbon dioxide. The author therefore believes that the *Chlorophyceae* exhibit a high CO_2 demand and the results of this investigation tend to support this contention. Carbon dioxide is required in photosynthesis and its presence in sufficient quantities will raise the hydrogen-ion concentration of the water indirectly by the formation of carbonic acid. In Quabbin Reservoir the two dominant classes, *Bacillariophyceae* and *Myxophyceae,* appear to interfere with development of green algae. This suggests that the nutritive requirements of these outstanding classes may be lower than those of the *Chlorophyceae.*

The 1 to 15 ratio observed between the *Chlorophyceae* and diatoms of the reservoir is in direct contrast with the results of the investigation of Coffing ('37) but the proportion compares favorably with the results of Allen ('20) and Kofoid ('08) for other bodies of water.

The 1.2% contributed by the *Chrysophyceae* to the total yield of net phytoplankton is a proportion similar to that arrived at by Damann ('41) for Lake Michigan. The summer pulse of *Dinobryon* is consistent with the findings of Bayliss and Gerstein ('29).

Ceratium and *Peridinium* are the only two genera of the *Dinophyceae* found in quantitative collections by several investigators (Daily '38, Damann '41, Gottschall and Jennings '33) from a variety of lakes. These two forms were also the only representatives of their class observed during this study. Little or no significance can be attached to the presence of *Dinophyceae* or of *Xanthophyceae* and *Euglenophyceae* as they were rare and sporadic.

Fluctuations of total net phytoplankton were closely correlated with dissolved oxygen, carbon dioxide, and hydrogen-ion concentration. An increase in dissolved oxygen and a decrease in both free carbon dioxide and hydrogen-ion concentration accompany phytoplankton increases. The supply of either of the gases mentioned may act as a limiting factor (Pearsall '23, Patrick '48) and the specific requirements of different forms for oxygen and carbon dioxide vary (Eddy '27b).

The quality of an aquatic microflora, just as with the higher plants, is greatly influenced by the pH of the water and a circumneutral range such as found for Quabbin Reservoir usually supports the greatest diversity of species. The indirect effects of pH on solubility of various substances should also be considered as having an important bearing on the types of organisms inhabiting a body of water.

Temperature and bright sunshine show some correlations with the curve for total yield (figs. 2, 5). Temperature seems to be a primary factor influencing the production of most forms. Apparently there are optimum temperatures for most of the genera encountered although several of the forms obviously tolerate a wide temperature range. The effect of temperature seems to be indirect as well as direct. Indirectly the temperature affects bacterial activity and solubility of gases and salts. Abundance of phytoplankton has been found by several other workers (Kofoid '08, Allen '20, Pearsall '22, Roach '32, Coffing '37) to be intimately linked with temperature although, as they point out, this factor does not necessarily play a lone role in algal periodicity.

The divergencies that exist between hours of sunshine and population pulses are striking in view of the positive correlation that persists for much of the survey. The discrepancies are manifest when those types which grow well at low light intensities are present; the parallelism continues while the growth of those forms

which grow well in abundant light is not retarded by physical-chemical deficiencies of the environment.

In light of conclusions arrived at by other workers (Pearsall '32, Chandler '40) on bodies of water similar to Quabbin Reservoir the decrease in silica observed in this survey prior to a diatom peak is not unusual. However, Meloche and co-workers ('28) observed the silica of Lake Mendota, Wisconsin, to decline following a diatom bloom.

It is apparent that periodicity of the net phytoplankton is influenced by many factors and that many genera are specific as to their requirements. The population increases seem to be limited or enhanced by competition among the forms of organisms and by the prevailing physical-chemical conditions.

Summary

1. A quantitative study of the net phytoplankton of Quabbin Reservoir undertaken from May 6, 1948 to October 30, 1948 revealed a marked periodicity for the total plankton and for the 7 classes and 68 genera observed.

2. A maximum weekly yield of 1,012 organisms per milliliter was recorded on June 17 and found to be 98.7% diatoms. A minimum of 166 per ml occurred on August 11 when the *Chlorophyceae* were at their peak (22.6% of yield).

3. The *Bacillariophyceae* dominated all but four of the weekly collections averaging 79.5% of the total net phytoplankton. *Myxophyceae* which averaged 14.1% of the total yield was more abundant than any other class during the last four weeks of summer. *Chlorophyceae* and *Chrysophyceae* were responsible for 5.4% and 1.2% respectively of the total, while *Dinophyceae, Xanthophyceae,* and *Euglenophyceae* yielded only a small fraction of 1%.

4. Throughout the survey each genus displayed its own pulses. Population peaks of the total free floating algae were normally the results of considerable increases in only one or two genera.

5. Temperature of the water may be a factor affecting the periodicity of many forms but it cannot account for the relative abundance of all net phytoplankton.

6. Hours of bright sunlight appear to have a correlation with spring and early summer maxima of phytoplankton but the quantity of light does not seem to be the controlling factor in algal periodicity.

7. The population pulses were accompanied by an increase in dissolved oxygen and pH and by a decrease in free carbon dioxide. Fluctuations in dissolved oxygen and carbon dioxide were the results of photosynthesis while pH seemed to be governed by the amount of free carbon dioxide present. The circumneutral range of the reservoir's water evidently permits a great diversity of forms.

8. Silica may be a limiting factor in the periodicity of the *Bacillariophyceae* since soluble silicates decreased prior to diatom pulses but demonstrated no correlation with members of other classes.

9. Manganese was absent from the epilimnion during the entire period of the study.

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BIOGEOGRAPHIC REGIONS OF TEXAS AND OKLAHOMA

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The ecologist who travels through Texas and Oklahoma might assume that the area could be easily divided into regions which are biotically distinct. The transitions from humid east to arid west and from subtropical south to cool north produce some very obvious patterns of distribution of flora and fauna. In spite of this obvious pattern, published records indicate many differences of opinion on both the location and description of the biogeographic regions or major biotic communities of these states. A few of these differences are more apparent than real because of variations in terminology or intensity of investigation. Other differences can be interpreted only as fundamental disagreements on what constitutes a major biotic community. The question that has not been answered is: how different must the fauna and flora of two areas be before they are recognized as examples of different communities?

Many of the differences result from attempts to separate communities by a line drawn on a map. Typical examples of communities are relatively easy to separate, but the separation is difficult in the gradual transitions or ecotones between communities. For example, Taylor ('45) lists 28 species of mammals as characteristic of Eastern Texas. A composite map of the ranges of these species emphasizes that no two species have identical limits of distribution. The short-tailed shrew (*Blarina brevicauda*) is limited to the extreme eastern portion of Texas; the gray squirrel (*Sciurus carolinensis*) occurs nearly 200 miles farther west; and the mink (*Mustela vison*) is found more than 300 miles west of the short-tailed shrew. If these species are characteristic members of a biotic community what is the geographic limit of the community?

Quantitative methods must be developed before general agreement on the extent of the major biotic communities can be reached. As long as personal opinion and individual judgment are the only bases for judging the extent of the communities, fundamental and insoluble differences of opinion will continue. In addition, quantitative determinations would be especially useful in many phases of applied ecology to indicate the extent to which ecological research can be applied, as in the development of land use programs.

In the course of an ecological reconnaissance of Texas and Oklahoma, the author developed a quantitative method for expressing some of the features of biological similarity between areas. The method is presented at this time in the hope that it will be tested on other areas to determine its values.

The method is a simple mathematical analysis of the distribution of a group of species. The results are expressed in terms of the degree of similarity of species composition between sample points. If two areas have identical species composition, they have a similarity value of 100; if the areas have no species in common, their similarity value is 0. The area studied is covered by a grid of sample points, and the species composition at each point is determined from species distribution maps. The similarity values computed for all adjacent points are plotted on a map. Areas with high similarity values have slight changes in spe-

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cies composition and at least indicate areas that Cain ('47) would call natural areas—a geographic unit with sufficient common characteristics to be of some usefulness in biogeography. However, when adjacent sample points have a low similarity value, the area is transitional between communities.

The method is applied in the following steps:

1. Determine and map the range of each of the species to be used in the computations. It would seem desirable to use as many species from as many taxonomic groups as possible, although to date the method has been used on only a few groups because of the lack of accurate distribution maps.

2. Prepare an overlay map on tracing paper on which the grid of sample points is marked.

3. Determine the species which occur at each of the sample points (i.e., a species list for each point).

4. For each pair of sample points, determine the number of species found at both the points (i.e., common to both), and the number of species which occur at only one of the two points (i.e., exclusive).

5. Calculate the similarity value for each pair of adjacent points by use of the formula:

$$\text{similarity value} = \frac{C \times 100}{T}$$

where C is the number of species which occur at both of the pair of sample points, and T is the total number of species which occur at either or both of the sample points.

6. Plot each similarity value on a map in its proper location between the two sample points used in the computation.

7. Draw lines on the map to indicate areas of equal similarity in the same way that contour lines connect points of equal elevation or isobars show areas of equal barometric pressure.

This method has been applied to the distribution of mammals in Texas and Oklahoma. Maps of mammalian distribution were traced from manuscript material made available by Dr. W. B. Davis, Professor of Wildlife Management, Agricultural and Mechanical College of Texas. Grateful acknowledgment is made for the use of this material before publication (Davis, '50).

An attempt was made to determine the most satisfactory interval for the spacing of sample points. An interval of 50 miles did not prove satisfactory because the mammalian similarity values then tended to be quite high over the whole area. However, an interval of 100 miles between sample points gave mammalian similarity values which ranged from 49 to 93. It now appears that the interval must depend on the rapidity of change in species composition in the particular area under investigation.

Other variations in application may be necessary because of the changes in faunal similarity values along the north-south or the east-west axes of the grid of sample points. For example, there are significant differences between the variances (indicated by the standard deviations) along the two axes for Oklahoma. The data (table I) indicate that the mean north-south faunal similarity value for Oklahoma mammals (80.65) is higher than any other and that the variance (standard deviation 5.4) is much lower than any other. In this case, it is important that the range from highest to lowest be great enough to indicate the transitions. As the standard deviation is a measure of the amount of variation, a statistical analysis was made to determine whether the north-south and east-west data were comparable in this regard. This statistical analysis indicates that the standard deviations for the north-south data and for the east-west data for Oklahoma mammals are very significantly different ($t = 2.891$; probability less than 1%), while the standard deviations for Texas mammals along the two axes are not significantly

TABLE I. *Mammalian faunal similarity values for Texas and Oklahoma, and faunal similarity values for snakes in Texas*

	Texas mammals			Oklahoma mammals			Texas snakes		
	east-west	north-south	total	east-west	north-south	total	east-west	north-south	total
Mean	66.25	73.92	70.08	69.19	80.65	74.00	71:25	79.62	75.44
Standard Deviation	11.9	10.6	11.8	9.2	5.4	9.6	10.5	7.7	10.1
Standard Error	2.42	2.16	1.70	1.53	1.06	1.23	2.15	1.57	2.06
Coefficient of Variation %	18.0	14.3	16.8	13.3	6.7	13.0	14.7	9.7	13.4

different ($t = 0.565$, probability more than 50%).

When all the Oklahoma data are plotted on the map, these facts are confirmed. The east-west faunal similarity values are variable and fall into a clear-cut pattern, while the north-south values are consistently high, indicating a very gradual change in species composition from the southern to the northern boundary of the State. This conclusion is in agreement with Snider ('17), Blair and Hubbell ('38), and Bragg and Smith ('43). For these reasons the north-south mammalian faunal similarity values for Oklahoma have not been used in the preparation of figure 1.

When the mammalian similarity values are plotted and the lines drawn, it is clear that there are four areas of high mammalian similarity (fig. 1). These four areas are believed to be the major biotic communities of Texas and Oklahoma. They may be called the eastern forest community, the Rio Grande Plain community of South Texas, the Trans-Pecos community of west Texas, and the High Plains community of the panhandles of both Texas and Oklahoma. Between these areas of relatively stable species composition are large transition zones where the mammalian faunas of the major communities mingle. It seems best to designate these as ecotones and not as communities, because the species present are largely those which are present in several communities or are those which are near the limit of their range. Although a few species appear to be characteristic of and limited to these transition zones, the number of such species is small.

The similarity values for other groups of vertebrates found in Texas have been made from the maps presented by Brown ('48). For each group the faunal similarity map shows considerable agreement with that prepared for mammals. In general those groups represented by fewer species show the greatest deviation from the more detailed mammalian map. The snakes are represented by a considerable number of species and the faunal similarity map for this group (fig. 2) shows a similar eastern forest community and an almost identical Trans-Pecos community. The High Plains community is similar, but extends farther south on the Edwards Plateau. The Rio Grande Plain community is poorly developed.

Statistical comparison of the faunal similarity values for snakes and mammals provides interesting information. The paired data were analyzed by the methods suggested by Snedecor ('46). The east-west faunal similarity values of snakes and mammals are from the same supply ($t = 1.55$, probability more than 5%) and there is a significant correlation coefficient r of 0.528 (probability of r being 0 is less than 1%). Conversely the north-south values for snakes and mammals are not statistically similar ($t = 2.13$, probability less than 5%) and there is a nonsignificant correlation coefficient of 0.251 (probability of r being 0 is approximately 25%). When both the north-south and the east-west faunal similarity values are combined, the snake and mammal data are not statistically similar

($t = 2.39$, probability approximately 1%), but there is a significant correlation coefficient of 0.495 (probability of r being 0 is less than 1%).

These statistics confirm the general agreement between figures 1 and 2, and they emphasize the possibility of differences in faunal similarity values taken in different cardinal directions.

The four major biotic communities recognized differ significantly in climate, physiograpy and soil as well as in the more obvious differences in species composition and life form of the vegetation. The reasons for the limitation of these communities to their present range are not obvious. The community of each area is made up of species which are usually not restricted to the area but which occur there in unique association. The eastern forest community, for example, includes several plant and animal species that are present in or dominant in other communities. Because the constancy of species composition, not the presence of an exclusive or endemic group of species, deter-

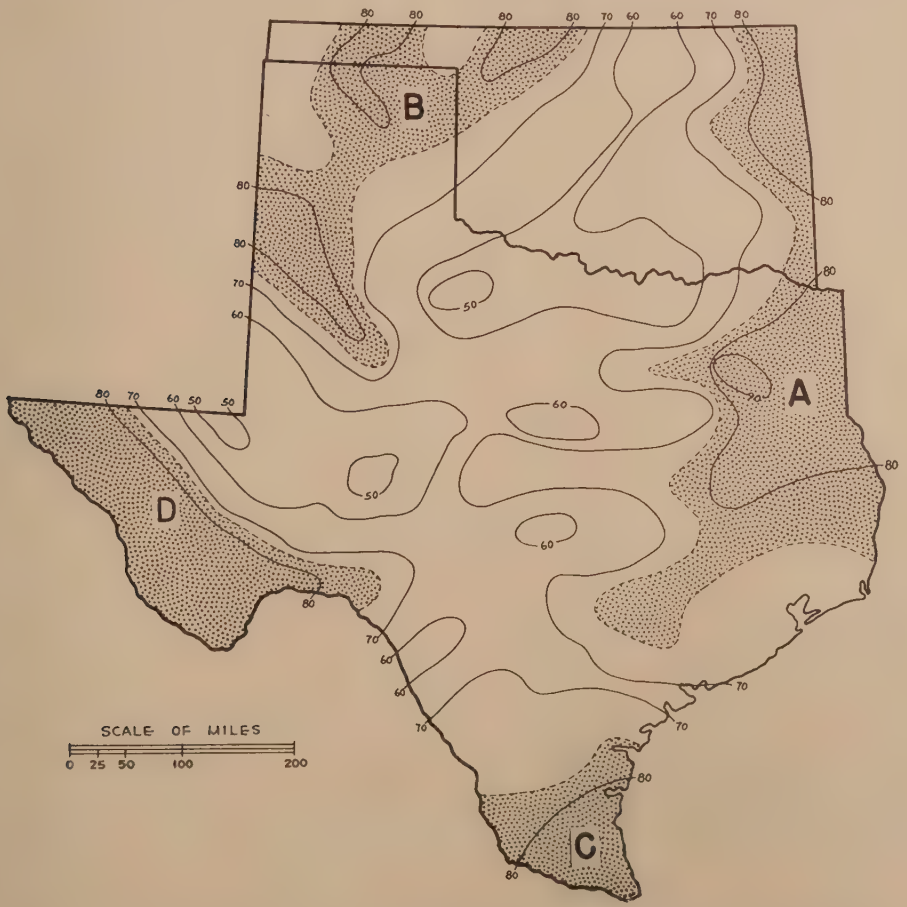

FIG. 1. Faunal similarity values for mammals in Texas and Oklahoma (data from Davis, '50). Regions with similarity values of 75 or more indicated by shading: A. Eastern Forest Community, B. High Plains Community, C. Rio Grande Community, D. Trans-Pecos Community.

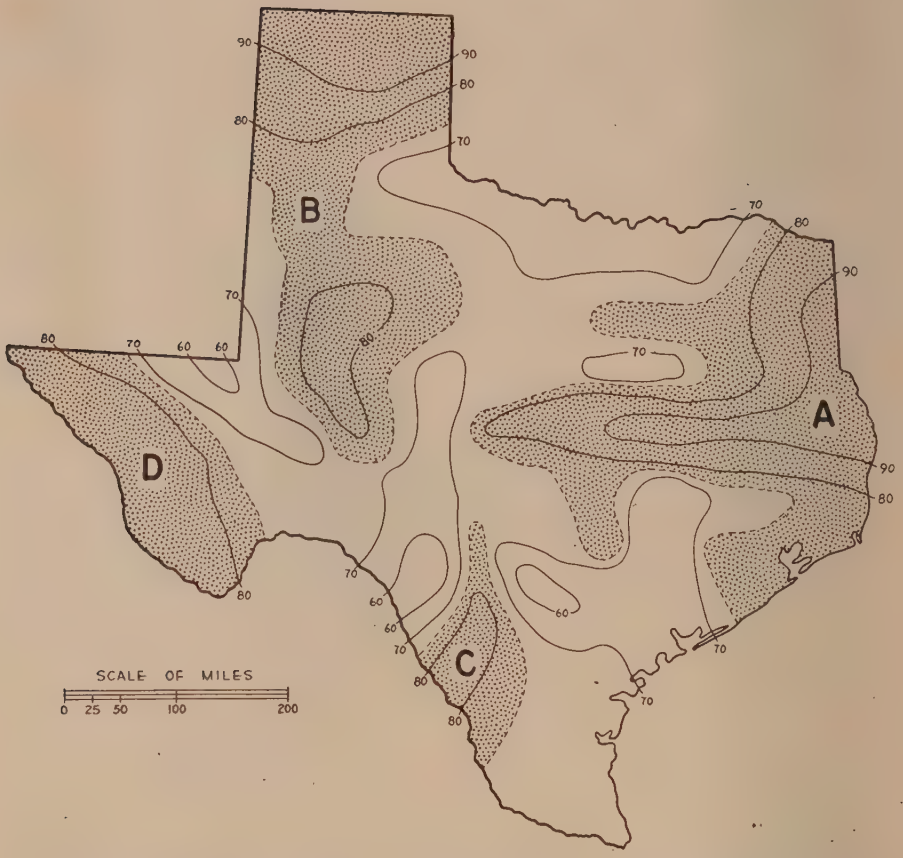

FIG. 2. Faunal similarity values for snakes in Texas (data from Brown, '48). Regions with similarity values of 75 or more indicated by shading: A. Eastern Forest Community, B. High Plains Community, C. Rio Grande Community, D. Trans-Pecos Community.

mines the geographic limits of the community, no attempt is made here to list characteristic or indicator species.

It is difficult to determine which environmental factor or group of factors is dominant in limiting a biotic community. Taylor has said that "The individual plant or animal integrates the environmental factors effective upon it and measures its own environmental factor complex better than any instrument or battery of instruments," and therefore ". . . the community is the most adequate measure of the forces of which it is in large part a product." [2] The four mammalian faunal similarity areas are correlated with the general distribution of climatic, edaphic, and physiographic features. This general agreement is not offered as proof of a cause and effect relationship. Further refinement of data and research on community distribution may indicate that some as yet unmeasured factor is the actual limiting factor.

Climatically the areas can be separated on the basis of rainfall and temperature:

[2] These quotations are from an unpublished manuscript by W. P. Taylor.

Trans-Pecos—average annual precipitation less than 15 inches; average frost-free period more than 200 days.

Eastern Forest—average annual precipitation more than 40 inches; average frost-free period more than 200 days.

High Plains—average annual precipitation less than 24 inches; average frost-free period less than 200 days.

Rio Grande Plain—average annual precipitation 20 to 40 inches; average frost-free period more than 280 days.

These relations may be of great importance in limiting the areas of high mammalian faunal similarity both by direct action on the animals and by indirect action through vegetation which provides food and cover. Composite climographs for each of the U. S. Weather Bureau stations within the four mammalian faunal similarity areas indicate that the climates of the areas may be of major importance in limiting the communities (fig. 3).

There is only a general relationship between the four areas of high mammalian similarity and the climatic provinces of the Koeppen system (James, '35), the climatic provinces recognized by Russell ('45), or the climatic provinces of

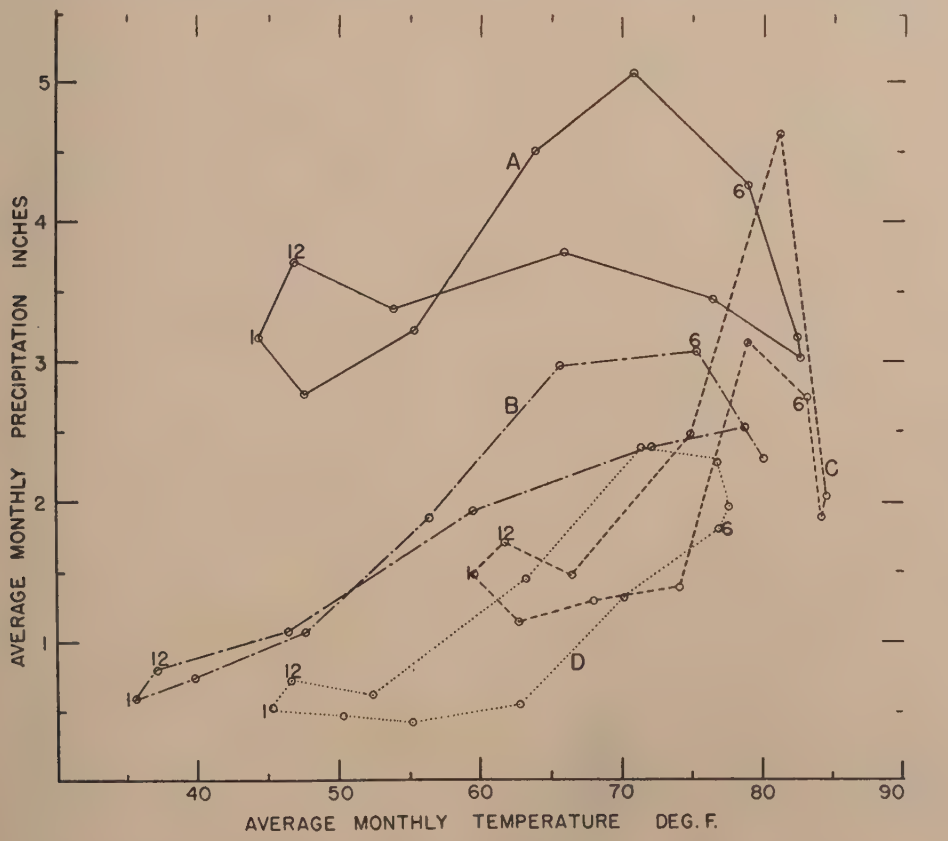

Fig. 3. Composite climographs for the U. S. Weather Bureau stations in the four areas of high mammalian faunal similarity. Climograph A for Eastern Forest based on 32 stations, Climograph B for High Plains based on 16 stations, Climograph C for Rio Grande based on 9 stations, and Climograph D for Trans-Pecos based on 5 stations. Monthly means indicated by 0; 1—January, 6—June, 12—December, etc.

Thornthwaite ('31). The more recent system proposed by Thornthwaite ('48) based on temperature, precipitation, and potential evapotranspiration provides data which may prove more helpful in determining whether climate may be the cause of changes in the faunal similarity values.

The physiography and soils of Texas and Oklahoma are varied and it is therefore difficult to determine their importance in controlling the distribution of the major biotic communities. The physiographic provinces (Fenneman, '31, and '38) and the soil types (Carter, '38) show some general relations to the areas of high mammalian faunal similarity. Detailed studies of these factors, and the climatic factors and their influence on species and community distribution, would probably indicate that the entire complex of environmental factors must be understood in order to determine the reasons for the limitation of the community to its present range.

Comparison of the areas of high mammalian faunal similarity with the biotic communities of various authors is complicated by the divergence of terminology and variation in intensity of study. There is very little agreement between figure 1 and the life zones used by Merriam ('98). The map of vegetation presented by Shreve ('17) shows some correlation with the areas of high mammalian faunal similarity. Grouping of similar vegetation types and separation of Shreve's transition types indicate many points of general agreement.

The Biotic Provinces recognized by Dice ('43) are in considerable agreement with the mammalian faunal similarity areas:

Faunal similarity area	Biotic province
Trans-Pecos	Chihuahuan
High Plains	Kansan
Rio Grande Plains	Tamaulipan
Eastern Forest	Carolinian and Austroriparian

Dice's Texan and Comanchian Biotic Provinces fall within the transition area where the faunal similarity values are low. These Biotic Provinces are characterized by Dice as being an intermingling of prairies and groves (Texan) or ". . . grassland in which shrubs and low trees grow singly or in masses" (Comanchian) (Dice, '43). The faunal similarity data suggest that these provinces do not have a stable mammalian fauna, but instead they are the ecotone where species from the several communities mingle and where many species ranges have their limit.

The distribution of biomes in Texas and Oklahoma as indicated by Pitelka ('41) shows some agreement with the four areas with high mammalian faunal similarity. The eastern forest area is clearly the deciduous forest biome and its oak-pine and pine subclimaxes. The High Plains area lies within the grassland biome. The Trans-Pecos area and the Rio Grande Plains area both fall within the desert scrub subclimax of the grassland biome. The Trans-Pecos area also has a considerable representation of piñon-juniper and interior chaparral. The areas which have the lowest mammalian faunal similarity values lie within the deciduous forest-grassland ecotone and at the edges of the grassland biome on Pitelka's map.

The areas of high mammalian faunal similarity show a close agreement with several state-wide surveys of biotic conditions. Taylor ('45) mapped and described four regions of mammalian distribution in Texas. If an area had been designated as an ecotone between these regions, very nearly perfect agreement with the areas of high faunal similarity would have resulted.

In Oklahoma, surveys of the distribution of plant communities by Bruner ('31) and of the distribution of biotic communities by Blair and Hubbell ('38) show considerable agreement with the mammalian faunal similarity areas. Data presented by Blair ('39) emphasize the gradual east-west transition in species composition and the mingling of eastern and western species in Central Oklahoma.

The most detailed study in either state

is the "game type map" of Duck and Fletcher ('44). The field mapping was done on county maps with a scale of 1 inch to 2 miles. Dice's Biotic Provinces and the areas of high mammalian faunal similarity show a considerable agreement with general features of the detailed map presented by Duck and Fletcher.

Summary

1. Quantitative methods are needed to aid in determining the extent of major biotic communities or biogeographic regions.

2. A simple quantitative method is proposed. This method is based on the degree of similarity of species composition at sample points.

3. When applied to the mammals of Texas and Oklahoma there are four regions with relatively stable species composition, with an extensive area of transition or ecotone between. These are: (a) eastern forest community, (b) High Plains community, (c) Rio Grande community and (d) Trans-Pecos community.

4. These four areas differ in climate, physiography, and soil; however, it is not possible to determine which factors of the environmental complex are responsible for the separation of the area into four regions.

5. There is considerable agreement between the Biotic Provinces of Dice ('43) and the four regions of high mammalian faunal similarity.

6. Several state-wide studies of ecologic types or studies of distribution of fauna and flora show general agreement with the four regions proposed.

7. It is hoped that the method used will be tried in other areas to determine its suitability as a technique for quantitative recognition of major biotic communities.

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THE INTERRELATIONS OF CERTAIN ANALYTIC AND SYNTHETIC PHYTOSOCIOLOGICAL CHARACTERS[1]

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Introduction

In the development of plant ecology, as in the development of other natural sciences, the early stages were concerned mostly with qualitative descriptions. With increasing knowledge the quantitative aspects increased, as descriptions were rendered more precise through the use of numerical measurements and indices. Many of the first "quantitative" studies were based upon ocular estimates of certain vegetational characteristics, rather than on exact numerical measurements. This was due largely to the realization that the great complexity of plant communities called for a large scale sampling of extensive areas instead of an intensive study of a few examples. The number of samples required often made it difficult or impossible to obtain the necessary data with a desirable degree of precision. Most ecologists have recognized that estimation by eye is not a suitable substitute for counting, weighing or other forms of direct measurement. Accordingly, many methods have been developed to expedite the collection of field data which may be handled by regular mathematical and statistical procedures.

The most important vegetational attributes which may be measured readily are size, number, and distribution in space of the component plants. Clements, at the turn of the century, recommended the use of small, square areas (quadrats) of known size as the basic study units for the investigation of these attributes. The almost universal acceptance of the quadrat method has provided a great wealth of data about plant communities in all parts of the world. The possible uses of the quadrat have been multiplied extensively in the hands of various workers; quadrats are regularly employed to determine such vegetational characters as frequency, density, abundance, and constancy. As might be expected, these adaptations have received their share of criticism. The objections largely stem from the fact that the size of the quadrat used directly influences the magnitude of certain of the resulting measurements. Because of this, various authors have recommended that these characters themselves be abandoned by phytosociologists. For example, Weaver and Clements ('38) say, "It has been shown that frequency depends so much upon the size of the quadrat employed as to be without value by itself." Such an extreme view is scarcely tenable, since the same thing could be said about measurements of length with a ruler or measurements of temperature with a thermometer. The recorded figures are of no value by themselves but are useful only when associated with scale units of definite and known size. The criticisms of density and constancy are similarly based upon this lack of appreciation of the relations between the size of the measuring unit and the magnitude of the resulting measurement. Admittedly, the interrelations are not as simple as in the linear relationship of the ruler or the thermometer, since the area of the quadrat increases as the square of the length of the side. However, the various attributes measured with the quadrat are mathematically related to one another, and a knowledge of these interrelations is essential for proper interpretation of results obtained with the quadrat method.

The nature of the interrelations has

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been demonstrated in the past by two main lines of approach. One of these has made certain assumptions about the random dispersion of plants and has developed the interrelations on a strictly theoretical basis, using the mathematics of probability (Gleason '20, Kylin '26, Blackman '35, and others). The other approach has been through the use of artificial populations (such as colored beads or colored cards) and actual sampling on a small or laboratory scale (McGinnies '34, Penfound '45). In this case, the interrelations were derived from the experimental results. Both lines of approach have their weaknesses, the first in the assumptions of randomness and the second in the lack of correspondence between the artificial populations and actual plant populations in nature.

Preston ('48) has shown that natural populations of a variety of kinds of organisms have a numerical structure which can be represented by a log-normal or log-Gaussian curve. With this structure as a model it is possible to construct artificial populations which closely resemble those in nature, at least insofar as the number of species and individuals are concerned. The present paper attempts to use such an artificial population to demonstrate the mathematical interrelations between certain analytic and synthetic community characters and to show how the relations are affected by the randomness or non-randomness of the component species. As will become apparent, many of the demonstrations merely confirm the work of earlier investigators who arrived at the same results by other means. It is felt that this repetition is justified since there has been no synthesis of these relations in the recent American literature, although Ashby ('36, '48) and Penfound ('45) have ably presented certain aspects of the problem.

Terminology

The main phytosociological characters to be discussed are frequency, density, abundance, constancy, and presence. A portion of the current uncertainty in phytosociology is due to lack of uniform usage of these terms by various writers, and to the indiscriminate use of synonyms for them. Thus frequency was called valence by Raunkiaer ('34) and McLean and Cook ('46), and frequency index by Gleason ('20), Potzger, Friesner, and Keller ('42) and Gates ('49). It is defined by most workers as the number of samples in which a species occurs, expressed as a percentage of the total number of samples examined.

$$\text{Frequency} = F = \frac{\text{No. of quadrats in which a species occurs}}{\text{Total no. of quadrats examined}} \times 100 \qquad (1)$$

However, Gates ('49: 35) also applied the term frequency to a determination of the number of individuals of a species found along a line, divided by the total number of all species, and later (p. 41) to the number of hits for each species by the point frame method, divided by the total number of hits for all species. Cottam and Curtis ('49) similarly extended the term in their random pairs method to indicate the number of points at which a species occurred divided by the total number of points examined. It is obvious that these diverse methods do not measure the same attribute and hence it is doubtful whether the same word should be used in all of them without qualification. In fact, a further exploration of the random pairs method by one of the authors (JTC) led to the realization that frequency as measured by that method was in fact different from frequency as measured by the quadrat method. The present study is a direct result of this belated recognition. Throughout this paper, frequency will be used to indicate quadrat frequency.

Density is used by many American and

European ecologists as a measure of the number of plant individuals per unit area.

$$\text{Density} = D = \frac{\text{Total no. of individuals of a species found}}{\text{Total area examined}} \qquad (2)$$

However, Braun-Blanquet ('28) clearly defined density as the total area examined divided by the total number of individuals found. This is the inverse or reciprocal of the first definition. Kylin ('26) called this reciprocal value the mean area (*Mittleareale*) of the plant.

$$\text{Mean area} = M = \frac{\text{Total area examined}}{\text{No. of individuals}} = 1/D \qquad (3)$$

Both concepts are extremely valuable and should be kept separate in terminology as well as in thought. Since the total area is often an odd value, densities and mean areas are commonly recorded in terms of standard units, such as square meters, acres, or hectares. A convenient method for comparative studies is to record density or mean area on a per-quadrat basis. This procedure is less liable to interpretive error than that using standard units, especially when the latter involves the expansion of figures determined on small areas to large units such as hectares. It is equivalent to measuring area in terms of quadrat-sized units. Hence, total number of quadrats examined may be substituted for total area examined in equations 2 and 3.

Abundance, as an ecological term, has been accorded a variety of meanings in the phytosociological literature. Braun-Blanquet ('28) and Gates ('49), among others, have used abundance as a rough indication of plentifulness, on the basis of estimation of numbers in five classes from "very rare" to "very abundant," McLean and Cook ('46) gave the word a special meaning. They summed the percentage densities per quadrat for each species and divided by the total number of quadrats. The result is thus the average percentage density and is a purely relative term; but it is based on actual density counts, not on estimates.

Abundance was used by Weaver and Clements ('38), Hanson and Whitman ('38) and other workers as an estimate of the number of individuals of a species per quadrat for the quadrats in which it occurred. It was determined in the field by estimating the plentifulness of individuals according to five unequal size classes (including an open-ended class of 100 or more), summing the estimates for all quadrats of occurrence, and dividing by this number of quadrats. Because of the nature of the size classes, abundance values had a maximum point of 100, regardless of the actual plentifulness of the individuals.

Several recent workers (Whitford '49, Cottam '49) have refined this last usage by replacing the estimation with an actual counting of the individuals. Abundance thus becomes the average number of individuals of a species per quadrat for the quadrats in which it occurs. As such it may be defined as:

$$\text{Abundance} = A = \frac{\text{Total no. of individuals found}}{\text{No. of quadrats of occurrence}} \qquad (4)$$

but:

$$D = \frac{\text{Total no. of individuals found}}{\text{Total no. of quadrats}}$$

and

$$F = \frac{\text{No. of quadrats of occurrence}}{\text{Total no. of quadrats}} \times 100$$

therefore:

$$A = 100D/F, \text{ where frequency is a percentage} \quad (5)$$

According to this if 10 individuals of a species are found in only one out of 10 quadrats examined the frequency would be 10.0%, the density 1.0, and the abundance 10.0, while if the 10 individuals were so distributed that one was present in each of the 10 quadrats, then the frequency would be 100%, the density still 1.0, but the abundance only 1.0. This usage has a definite value since it enables the relative randomness of a species to be determined directly from field data (Whitford '49).

Constancy is one of Braun-Blanquet's ('28) synthetic characters in that it is determined upon many stands of a given association, rather than within one stand only. Like quadrat frequency, it is a measure of ubiquity, on an interstand rather than an intrastand basis. It is arrived at by examining a single sample area of uniform size in each stand and determining the presence or absence of a species.

$$\text{Constancy} = C = \frac{\text{No. of samples (one per stand) in which a species occurs}}{\text{Total no. of stands examined}} \times 100 \quad (6)$$

In practice it differs from quadrat frequency, in that no two stands are actually identical and hence there is a floristic difference between the samples as well as a difference in the distributional pattern of the individual species (Kylin '26).

Presence is very closely allied to constancy and is determined in the same way except that the entire stand is examined rather than a measured sample of it (Braun-Blanquet '28, Curtis and Greene '49).

$$\text{Presence} = P = \frac{\text{No. of stands in which a species occurs}}{\text{Total no. of stands examined}} \times 100 \quad (7)$$

It suffers from a certain lack of precision in that the stands may be of different area and hence may contain different numbers of the very rare species. However, ecologists usually use stands of nearly similar size and thus tend to minimize this defect. The main difference between presence and constancy is that presence values are higher than constancy values for the same species when the constancies are less than 100%.

As given in the above formulas, frequency, constancy and presence values are ratios which are converted to percentage figures by multiplying by 100. Density may also be expressed as a percentage value. This is done by dividing the number of individuals of a given species by the total number of individuals of all species. Density per cent is thus totally independent of area, at least in its method of calculation, and is actually a relative term. It is perhaps best called *relative density*.

$$\text{Relative Density of species A} = \frac{\text{No. of individuals of species A}}{\text{Total no. of individuals of all species}} \times 100 \quad (8)$$

Frequency values were subjected to considerable manipulation by Raunkiaer ('34). Among the concepts he introduced was the percentage sum of fre-

quency, or *relative frequency*. This is the frequency value of a given species divided by the total of the frequency values for all species.

$$\text{Relative Frequency of species A} = \frac{\text{Frequency of species A}}{\text{Sum of frequency values for all species}} \times 100 \quad (9)$$

This procedure introduces a relative element and makes the value dependent upon those of the other species of the community. Because of this, the percentage sum of frequency does not lend itself to ready correlation with the other analytic or synthetic characters. Nevertheless, the relative nature of the measure makes it valuable in comparative studies, particularly when used in combination with density and dominance measures.

The other main analytical character commonly used in phytosociological studies is concerned with the size, bulk, or space demands of the plants. It is usually called dominance and includes such concepts as basal area, cover, volume or weight. Several methods are used in the determination of this character, varying from an optical estimate of cover at one extreme, to an exact measurement of basal area or weight at the other. The data are usually expressed either as absolute units per unit of ground area or as a relative figure given in per cent. There appears to be no way by which these dominance figures may be related to frequency or density, since there is no exact mathematical relation between them. Accordingly, they will not be mentioned further in this study. The same applies to the synthetic character of fidelity, which is a floristic character, quite independent of the number or relative dispersion of plant individuals, at least as defined by Braun-Blanquet ('28).

Methods

The artificial population used in this study was constructed on the basis of the log-normal population of Preston ('48). The "species" in this population were represented by various common objects such as seeds, thumbtacks, hex nuts, and paper clips, which could easily be recognized by their shapes. The numbers of individuals of the objects varied from two to 1,600, with the number of objects arranged according to Preston's curve so that there were few kinds with either very few or very many individuals and many kinds with intermediate numbers of individuals. These were divided into groups (or oc-

Table I. *"Species" composition of artificial population*

Species	No. of individuals	Octave	No. of species per octave	Average mean area per octave
Cabbage seed	1,600	K	1	4.0 cm²
Corn grain	800	J	2	9.7
Rivet	600			
Thumbtack	400	I	2	19.3
Staple	300			
Small hex nut	220	H	3	37.6
Wood screw*	180			
Small square nut**	140			
Dollar sign	100	G	4	80.9
Cents sign	88			
Number sign	75			
Letter 'x'	68			
Letter 'o'	60	F	4	147.1
Number 1*	54			
Number 2	42			
Number 3	34			
Number 4	30	E	5	304
Number 5	26			
Number 6	22			
Number 7	19			
Number 8	17			
Folding clip	15	D	4	542
Small washer	13			
Large washer	11			
T fastener	9			
Gem paper clip	7	C	4	1,117
Coffee tree seed	6			
Corrugated nail	5			
Large square nut	5			
Screw eye	3	B	3†	2,100
Safety pin	3			
Tubing clamp	2	A	1†	3,150
W paper clip	2			

* Clustered species
** Regular species
† Octave A is recorded as having only one species, and octave B as having three, because half of the doubletons are assigned to octave A and half to octave B (see Preston '48).

taves of Preston) on a $\log_2$ basis, each group containing objects with twice as many individuals as the preceding group, i.e. 1, 2, 4, 8, 16, 32, 64, 128, 256, 512, 1,024, 2,048. These numbers were used as boundaries between octaves, rather than as mid points. The modal octave in this array contained five kinds of objects with numbers of individuals varying from 16 to 32. The list of objects and their numbers are given in table I. The objects were laid out on a large piece of paper lightly ruled in 1″ cross sections numbered by row and tier. For most of the objects, the placement was made according to a random numbers table (Snedecor '46). The three most numerous objects were placed by simply scattering them over the surface of the paper. While absolute randomness could not be achieved with certainty by the latter method, trial results showed that a random condition was approached very closely. One type of object was arranged in a regular fashion on the corners of squares, while two types of objects were placed in dense clusters, with the clusters arranged randomly through the use of the random numbers table. These two clustered species differed in their absolute density. The population thus consisted of 33 species—one regular, two clustered, and 30 at random. The final array was photographed so that actual study could be made on greatly enlarged prints rather than on the objects themselves. In this way the danger of disarrangement by quadrat manipulation was avoided. A portion of the final print is shown in figure 1.

Sampling was accomplished by laying square quadrats of known size on the print. The quadrats consisted of sheets of transparent plastic, with the quadrat lines engraved on their surface. The quadrats were sometimes placed at random by a toss to the print and sometimes according

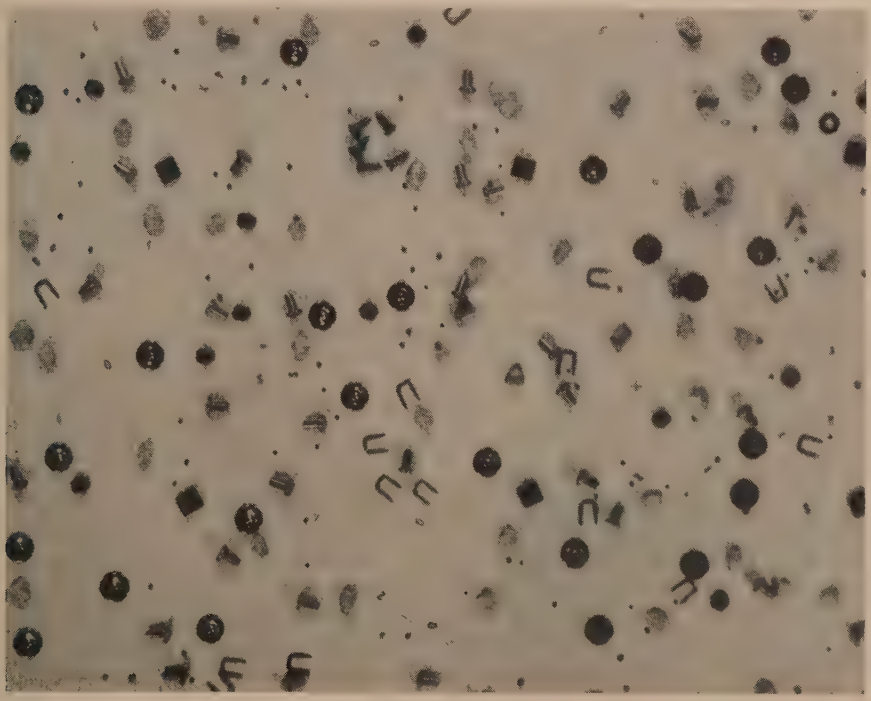

Fig. 1. Portion of a photograph of the artificial population.

to a regular pattern. An individual was taken to be in the quadrat if one half or more of its area was inside of the lines. Since the lines were very thin, only a small error was introduced by this method. Early trials, in which an individual was counted if any part of it touched the line, were not satisfactory since they gave over-representation, particularly of the more numerous species. The data, which were recorded on specially prepared blanks, included the kinds of species present, the number of individuals of each species, and the number of groups of the clustered species for each placement of the quadrat.

The size of the smallest quadrat used was exactly 0.50 times the mean area per plant of the most numerous species. Each successively larger quadrat was twice the area of the preceding one, with the largest being 128 times larger than the smallest. In addition to these sizes on a $\log_2$ basis, another set of $1\times$, $10\times$, and $100\times$ were used, so that values comparable to the usual 10 meter forest quadrat with the 1 meter herb quadrat in its corner (Eggler, '38) could be obtained. Altogether 10 sizes were used. For a given test at least 50 throws of each sized quadrat were made, although in some trials as many as 625 throws were used.

From the data obtained in this way, various phytosociological characters were calculated, including frequency, density, relative density, abundance, species density, relative frequency, and constancy. These characters were compared with one another in several ways, usually by plotting two or more of them on a graph. The nature of the interrelations was explored by use of various scales on the axes of the graphs, such as logarithmic, square root, and other transformations. In general, the most instructive curves were obtained when both species measures and quadrat sizes were plotted on a $\log_2$ scale. In many instances, the species information was averaged by octave groups after the manner of Preston and the averages used on the graphs.

Results

Theoretical interrelations if species are random

When the data from only the random species are used, several interrelations between analytic characters can be demonstrated. The basic relationship between frequency and density shown by the formula, $F = 100\ (1 - e^{-D})$, as proposed by Gleason ('20), Kylin ('26), Ashby ('35), Clapham ('36), Fracker and Brischle ('44), and others is again shown by the present test. While this is not remarkable, it does lend additional confidence to

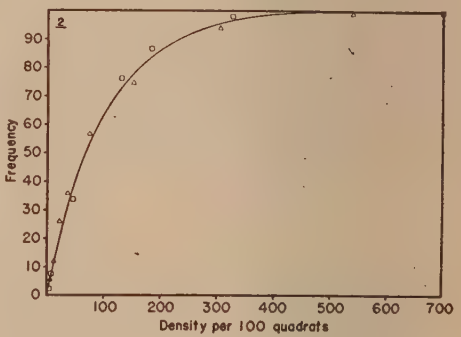

Fig. 2. The relation between frequency and density as determined by quadrats of different size. Squares—quadrat area equal to mean area per plant for species in the modal octave. Triangles—quadrat area equal to ⅛ the mean area per plant for the modal species. Solid line indicates theoretical relation for truly random population.

the use of Preston's log-normal population as a basis for such tests since the observed results agree very closely with the theoretical values. Figure 2 shows frequency plotted against density (number of individuals per 100 quadrats) for the quadrat size equal to the mean area per plant for species in the modal octave of the population and for the quadrat size one-eighth that large. The theoretical curve is also shown for comparison. This was calculated by aid of the formula,

$$D = 100 \log_e\left(\frac{100}{100 - F}\right),$$

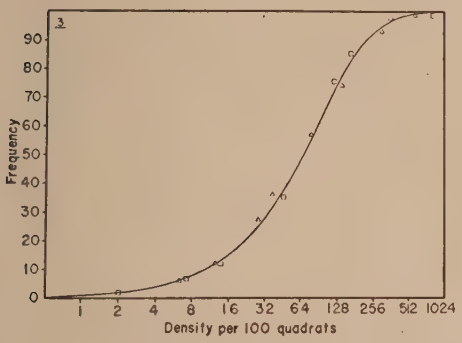

FIG. 3. Same as figure 2, but with densities on a $\log_2$ basis.

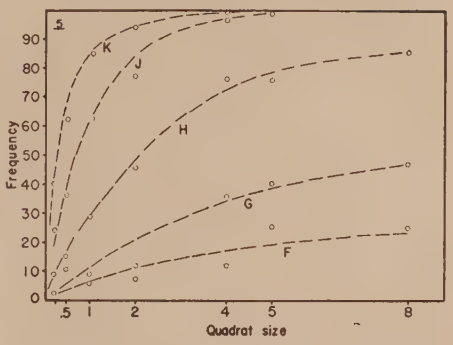

FIG. 5. The relation between frequency and quadrat size for several species of different densities. Broken lines through actual data from artificial population. The letters refer to the octaves as in table I.

as given by Fracker and Brischle ('44). In figure 3, the same data are plotted with densities on a $\log_2$ basis. Use of mean area per plant in quadrat-sized units instead of density is shown in figure 4 on a linear scale. Similar agreement between actual and theoretical values was obtained for all quadrat sizes, although the sampling irregularities were greater for the rare species when smaller quadrats were used.

The relation between frequency and quadrat size for several species of different densities, averaged by octaves, is shown in figure 5. Briefly stated, the curves indicate that frequency increases more rapidly with increasing quadrat size when densities are great than when densities are low. This relation is shown in a generalized way in figure 6 for mean areas per plant in quadrat-sized units instead of numbers of individuals per unit area. Some convenient rule-of-thumb reference points on this curve are listed in table II. Any other values may be calculated by the formula,

$$M = \frac{1}{-\log_e(1-F)}$$

(Ashby '35). The interrelations between frequency, density per quadrat, mean area in quadrat-sized units, and quadrat size are shown by the straight line in figure 7. This line can be used to determine density and mean area for any given frequency

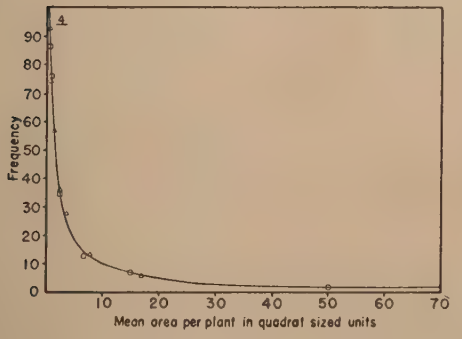

FIG. 4. The relation between frequency and mean area per plant for the same quadrat sizes as in figure 2.

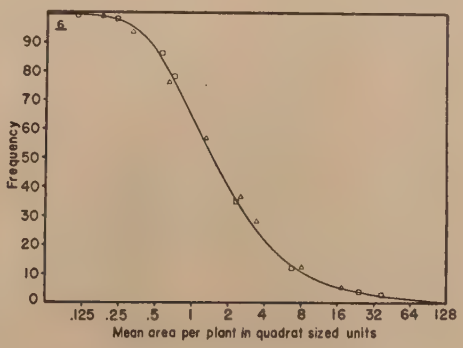

FIG. 6. Same as figure 4, but with mean areas on a $\log_2$ basis.

TABLE II. *Selected reference points for the relation between frequency and mean area per plant*

If the frequency is:	then the mean area is:
11.9 (ca 10)	8 times the quadrat area
22.1 (ca 20)	4 times the quadrat area
39.3 (ca 40)	2 times the quadrat area
63.2 (ca 60)	equal to the quadrat area
86.5	½ the quadrat area
98.0	¼ the quadrat area
99.9 (ca 100)	1/10 the quadrat area

and also to determine frequency at any quadrat size if its value is known for any other quadrat size.

On the basis of plant areas, the relation between quadrat size and relative frequency for selected species in the artificial population is shown in figure 8. As can be seen, relative frequency decreases rapidly with increasing quadrat size when the quadrats are larger than the mean area, and increases when the quadrat areas are less than the mean areas. All species with an area less than ¼ that of the quadrat area have approximately equal relative frequencies. As shown in table II, such species are those with a frequency of 100 or nearly that. This rather complicated relationship is due to the fact that the most plentiful species (i.e., those with small mean areas) show a high frequency even with very small quadrats and this cannot be increased beyond 100% regardless of an increase in quadrat size. On the other hand, the rare species have a low frequency with small quadrats and a larger frequency with increasing quadrat size. On a relative basis, therefore, they occupy a more prominent portion of the total when large sizes are used. Theoretically, with extremely large quadrats all species in the assemblage will have frequencies of 100%. Under such circumstances, all species will have the same relative frequency, with an actual value equal to 100 divided by the total number of species in the assemblage. Relative frequencies thus attain maximum usefulness when the quadrat size used is less than four times the mean area of the most numerous species.

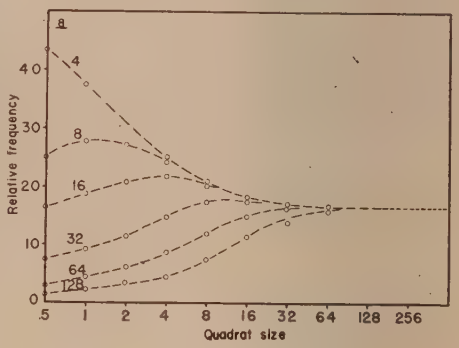

FIG. 8. The relation between relative frequency and quadrat size for species varying from 4 to 128 in mean area per plant in quadrat-sized units. Data from artificial population.

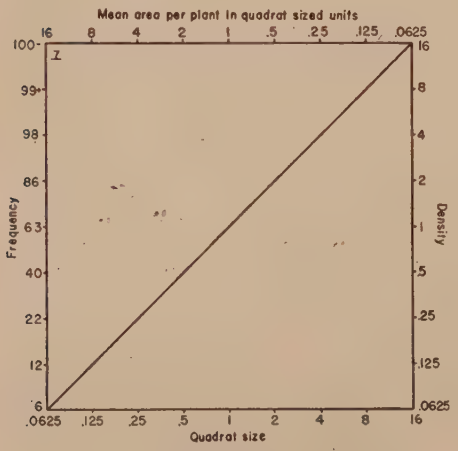

FIG. 7. Theoretical interrelations of frequency, density, mean area and quadrat size.

The total number of species recorded is affected by quadrat size in the manner shown in figure 9. While the number of species rises rapidly with the first few quadrats, regardless of quadrat size, the subsequent behavior is dependent on the quadrat size. When the quadrat is only one-half the size of the mean area of the most numerous species, the curve rises very slowly.

The number of species per quadrat, sometimes called the *species density,* increased with increasing quadrat size for

TABLE III. *Effect of quadrat size on percentage distribution of species in artificial population in Raunkiaer's frequency classes*

Quadrat size	Raunkiaer's frequency classes				
	1–20	21–40	41–60	61–80	81–100
0.5	88.2%	11.7%	0	0	0
1	85.8	10.7	0	3.6	0
2	72.4	13.8	6.9	3.4	3.4
4	73.3	6.7	6.7	10.0	3.3
8	56.3	18.7	3.1	6.2	15.6
10	50.0	16.7	6.7	10.0	16.7
16	43.8	12.5	12.5	6.2	25.0
32	33.3	13.3	13.3	10.0	33.3
64	22.6	12.9	12.9	9.7	42.0
100	12.9	16.1	12.9	3.2	54.8

the artificial population, as indicated in figure 10. The quadrat size which gave on the average 50% of the total number of species in the population was equal to ½ the mean area of the modal species.

Raunkiaer's "normal" curve of frequency is markedly affected by quadrat size, as shown by table III. This demonstration supports the conclusion reached previously by Kylin ('26), Gleason ('29), McGinnies ('34), Cain ('43) and Preston ('48), namely that increasing the quadrat size increases the number of species in the highest frequency class, while decreasing the quadrat size has the opposite effect. In view of the relations between frequency and plant area shown above, however, the "normal" curve may be given a more

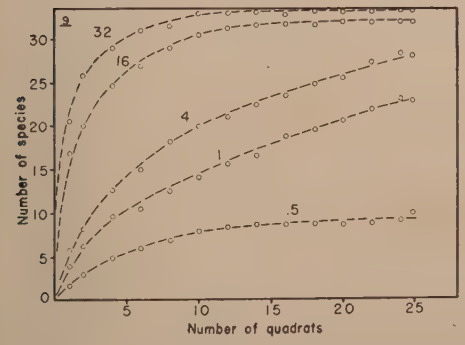

FIG. 9. The relation between number of quadrats and total number of species recorded for quadrat sizes varying from 0.5 to 32. Data from artificial population.

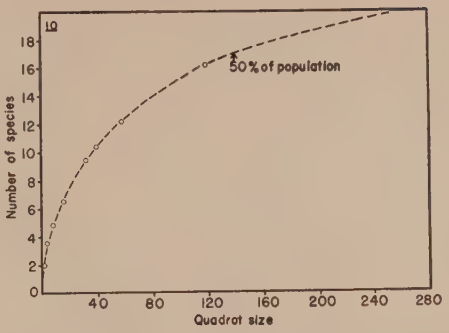

FIG. 10. The relation between number of species per quadrat and quadrat size. Data from artificial population.

useful interpretation. Species appear entirely in the smallest or 1–20% frequency class when the quadrats are approximately 0.20 times the size of the mean area of the most numerous species and in the highest or 81%–100% frequency class when the quadrats are 2.0 times the mean area of the least numerous species. Equal numbers of species are found in each of these frequency classes when the quadrat size is about ½ the mean area of the modal species. According to this interpretation, a Raunkiaer distribution does not indicate uniformity or homogeneity of an association or of a species assemblage as is commonly asserted, but merely indicates the distribution of species areas in terms of quadrat size. A given frequency distribution shows the number of species with mean areas smaller than, equal to, and larger than the quadrat area (table IV). Any given actual plant dispersion, of whatever degree of homogeneity, will show greatly differing Raunkiaer curves, if different sized quadrats are used. This does not mean that the Raunkiaer curve

TABLE IV. *Distribution of mean areas according to Raunkiaer's frequency classes*

Frequency class	Approximate mean area of species in quadrat-sized units
81–100%	½ or less
61–80%	½ to 1
41–60%	1 to 2
21–40%	2 to 4
1–20%	Over 4

is of no value. While it in no sense is a measure of homogeneity, it nevertheless can be used as an indication of the distribution of mean areas, and this is true, regardless of the size of quadrat used. Homogeneity is here taken to mean a distribution of species such that all will be represented with the same given probability in each sample of a suitable size. It necessarily implies that the individuals are randomly distributed or are in groups which themselves are at random. It does not mean that the species are so distributed that all will appear in each sample. Such a situation could occur only if each species had the same mean area as all the rest. Manifestly, no distributions of this sort appear in nature and hence such a concept is valueless.

Frequency-Constancy.—Constancy has been defined as stand-frequency. Since stands are presumed to be isolated portions of a uniform plant community, it follows that constancy data should show the same characteristics as intrastand frequency. The interrelations between frequency and constancy should be the same as those between frequencies at 2 quadrat sizes, if the species are random and the stands actually uniform. This relationship is given by the formula: $F_2 = 1 - (1 - F_1)^{Q_2/Q_1}$ where F_1 is the frequency (as a ratio, not a per cent) determined by quadrats of area Q_1 and F_2 the frequency at area Q_2 (Blackman '35). Thus if the second quadrat Q_2 is 16 times larger than the first quadrat, the second frequency will be $1 - (1 - F_1)^{16}$. Similarly, if the area used for constancy determinations is 16 times larger than that for frequency, then constancy will be $1 - (1 - F)^{16}$. In general terms:

$$\text{Constancy} = 1 - (1 - F)^{CQ/FQ} \quad (10)$$

where CQ is the constancy quadrat area and FQ is the frequency quadrat area.

These relations are shown in table V for quadrats of different size. Using the log normal population, very close approximations to theoretical values were obtained, except for the very rare species.

Frequency-Presence.—Frequency-presence interrelations could not be determined with the artificial population as the total number of species per "stand" was constant in all determinations, but since presence is measured on the entire stand rather than a unit portion of it, presence values are always higher than corresponding constancies, when the constancies are less that 100%. No conclusion about interrelations may be drawn if either presence or constancy values are 100%.

Frequency-Abundance.—As Whitford ('49) has pointed out, abundance is a valuable measure since it may be used to study the problem of dispersion. The theoretical relation of frequency to abundance is shown in figure 11 together with determinations made from the artificial population at several quadrat sizes. The agreement is good as would be expected from a consideration of figure 2, since $A = 100\ D/F$.

On many occasions, density values from field studies are available only as relative

TABLE V. *Change in frequency with increasing quadrat size (for random distributions)*

Frequency at size x	Frequency at size:										
	$2x$	$4x$	$5x$	$8x$	$10x$	$16x$	$20x$	$32x$	$50x$	$64x$	$100x$
1%	1.9	3.9	4.9	7.7	9.6	14.5	18.2	27.7	39.5	47.7	63.4
3%	5.6	11.5	14.2	21.7	26.3	38.5	55.5	62.2	78.2	85.7	95.3
5%	10	18.6	23	33.7	43.5	56.1	64.2	80.0	92.4	96.25	99.4
10%	19	34.4	41	57	65	81	86.8	96.6	99.5	99.9	—
20%	36	59	67.3	84	89.3	97	98.8	99.9	—	—	—
40%	64	87	93	98	99.4	99.9	—	—	—	—	—
60%	84	98	99.9	—	—	—	—	—	—	—	—
80%	96	99.8	—	—	—	—	—	—	—	—	—

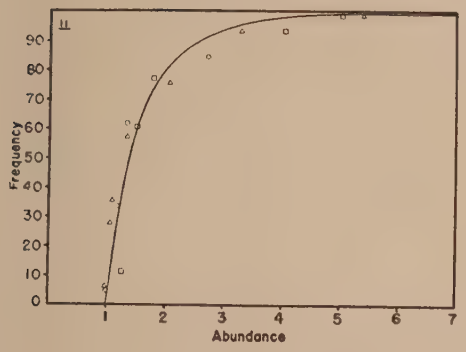

FIG. 11. The relation between frequency and abundance as determined by quadrats of different size. Squares—quadrat area equal to mean area per plant for species in modal octave. Triangles—quadrat area equal to ⅛ the mean area per plant for the modal species. Circles—quadrat area twice the mean area of the most numerous species. Solid line indicates theoretical relation.

densities. The interrelations of these values with frequencies are very similar to the frequency-density relations as regards the effects of quadrat size, but the absolute position of the curves is dependent upon the number of species in the population. For the artificial population of 30 random species, the relation to quadrat size is shown in figure 12. Populations richer in species would show an upward deviation of the curves, while species-poor populations would vary in the opposite direction for any given quadrat size.

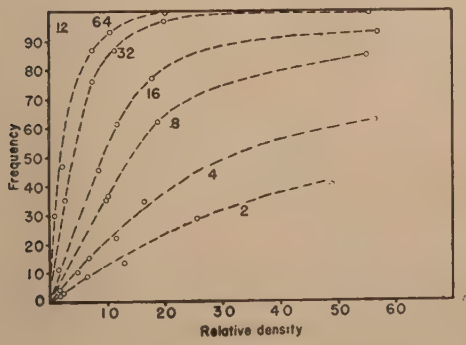

FIG. 12. The relation between frequency and relative density for quadrats varying in size from 2 to 64. Data from artificial population.

Relative accuracy of different characteristics.—Frequency, relative frequency, and constancy have been shown to be dependent upon quadrat size for their absolute numerical values. Density per quadrat and abundance per quadrat are similarly dependent. However, densities per unit of absolute area and relative densities are largely independent of quadrat size, provided only that a sufficient number of samples be used. This is shown in figure 13, where it may be seen that the relative density remains essentially constant, regardless of quadrat size, for species of greatly differing mean areas.

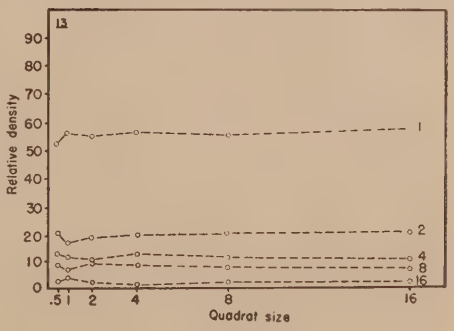

FIG. 13. The relation between relative density and quadrat size for species varying from 1 to 16 in mean area per plant in quadrat sized units. Data from artificial population.

The average coefficient of variation for the species shown was 10.93% with a range from 5.49% to 15.47%. In practice this means that one-tenth meter quadrats will give the same information as to relative number of plants as will one-meter quadrats, if enough are used to obtain figures of statistical significance.

Theoretical interrelations for non-random distributions

The above interrelations hold true only if the individual species in the assemblage are distributed at random and are sampled at random. From the results of many studies (Blackman '35), Fracker and Brischle '44, Ashby '48, Whitford '49, etc.) it is apparent that most species are

not randomly distributed, at least at some stage during their existence in a community. At first thought, this fact would appear to invalidate most of the relations of the preceding section. Actually, however, the existence of such mathematical relationships in random distributions makes it possible to detect the non-randomness of any particular species and to assess its degree of departure from the theoretical, random condition. If one of the analytical characters is determined in the field, then a corollary character may be predicted. If the actual field data for this second character do not agree with the prediction, then the difference between them becomes a measure of nonrandomness.

This general procedure was used by Blackman ('35), McGinnies ('34), Ashby ('35), Fracker and Brischle ('44) and Whitford ('49), with the first five using the basic frequency-density relation, $F = 100\ (1 - e^{-D})$, while Whitford used the frequency-abundance relation. Blackman made use of the Poisson distribution of numbers of quadrats occupied by 0, 1, 2, 3, etc. individuals, but was concerned mainly with the unoccupied samples, which form the first term of the series. In effect, Blackman compared actual field densities with theoretical densities as calculated by the formula, percentage absence $= e^{-D}$, where absence $(1 - F)$ was determined from the empty quadrats. McGinnies used a similar measure in that he compared actual densities with theoretical densities as calculated from frequency values. Deviation from randomness (K) is thus expressed by the formula:

$$K = D/d \qquad (11)$$

where D is actual density and d is expected density. Fracker and Brischle thought that the linear relation did not suitably fit their data and proposed the formula:

$$K = (D - d)/d^2 \qquad (12)$$

Whitford used the ratio of abundance to frequency (A/F) as a measure of randomness, since $A \times F = D \times 100$ and thus a given density may be the result of high frequency and low abundance or low frequency and high abundance. In the latter case, the species is clearly nonrandom and this is shown directly by a high value of the A/F ratio. In the notation used above, Whitford's measure becomes:

$$K = 100D/F^2 \qquad (13)$$

Clapham ('36) made use of a well known property of a Poisson series, namely, that the variance of all items is equal to their mean. He set up a ratio of variance (V) to the mean $(\bar{x})$ which he called the relative variance but which was more appropriately termed the *coefficient of dispersion* by Blackman ('42). For a perfectly random species, this coefficient would be unity (1.0).

$$K = V/\bar{x} \qquad (14)$$

All of these formulas are applicable to individual species and may be used to assess the deviation from randomness of any species for which experimental values for frequency and density are available. It is often desirable to record the departure from randomness for the entire complement of species in a given example of a plant community. There are several possible ways of doing this, but we propose the method which sums the individual densities of all species and the individual expected densities, as calculated from the actual frequencies, and then uses the ratio of the sums as a measure of average randomness:

$$K = \Sigma D/\Sigma d \qquad (15)$$

In this summation procedure, the final measure is weighted in the direction of the more plentiful species, but this seems proper in a general statement about a plant assemblage. The expected densities may be obtained readily from table I in Fracker and Brischle's paper ('44).

Other recent investigators (Neyman '39, Cole '46, Archibald '48) have elaborated on the statistical procedures to be used in determining the degree of non-

randomness. They have largely standardized on the use of Neyman's term "contagious," to indicate a non-random distribution in which the individuals are more closely bunched than normal. Situations where the individuals are more regular than would be expected by chance are called "regular" or "negatively contagious." These terms replace the earlier "overdispersion" and "underdispersion" which were used in opposite senses by various writers and had become a source of great confusion.

No detailed investigation of non-randomness was made in the present study. As indicated in the section on methods, two species of different density in the artificial population were placed in a contagious fashion, while one other species was placed in a regular or negatively-contagious pattern. The purpose of inserting these three species was to obtain data on the behavior of non-random species in comparison with the random population. The absolute density of the second contagious species unfortunately was so low as to give rise to rather large sampling errors, with consequent large fluctuations in the data.

The degree of non-randomness of the three species was determined for the several measures described above (D/d, $(D-d)/d^2$, $100D/F^2$, and $V/\bar{x}$). The results are summarized in table VI. As can be seen, not all methods give similar results under all conditions. For truly random species, all but Whitford's $100D/F^2$ are independent of quadrat size. The $100D/F^2$ measure gives minimum values for the random species when the quadrat size is equal to the mean area. All measures are dependent on quadrat size when the species are contagious. It appears that peak values are usually reached when the quadrat size is equal to the mean area, but the data are not conclusive on this point because of sampling irregularities. In the case of regular species, the D/d, and $100D/F^2$ measures reach a minimum value when plant area and quadrat area are about equal, while $(D-d)/d^2$ and $V/\bar{x}$ values get progressively smaller as

TABLE VI. *Relative randomness of selected species as measured by different methods*

Species and method	Quadrat size							
	1	2	4	8	16	32	64	128
Contagious 1								
D/d	2.16	1.56	2.60	3.72	3.82	3.68	3.68	3.74
$100D/F^2$	.360	.173	.199	.233	.210	.137	.091	.097
$V/\bar{x}$	1.08	1.74	3.12	3.78	4.13	3.47	3.34	3.72
$(D-d)/d^2$	.178	.051	.106	.140	.124	.068	.023	.015
Contagious 2								
D/d	1.00	1.00	5.00	4.00	3.60	2.72	5.00	2.19
$100D/F^2$	1.00	0.250	5.00	1.33	0.27	0.15	0.41	0.06
$V/\bar{x}$	0.990	0.960	4.948	4.385	3.790	3.135	4.105	2.500
$(D-d)/d^2$	—	—	4.00	1.00	.172	.076	.294	.016
Regular								
D/d	1.00	0.90	0.89	0.82	0.63	0.46	0.67	0.74
$100D/F^2$	.333	.057	.043	.028	.015	.014	.026	.051
$V/\bar{x}$	0.970	0.829	0.805	.575	.446	.256	.250	.083
$(D-d)/d^2$	—	.0046	.0045	.0043	.0029	.0019	—	—
Random*								
D/d	1.023	1.017	1.100	1.085	0.973	1.067	1.137	1.142
$100D/F^2$	0.303	0.085	0.076	0.070	0.031	0.029	0.036	0.042
$V/\bar{x}$	0.949	0.931	1.280	1.055	0.888	1.000	1.118	0.739
$(D-d)/d^2$	.0018	.0023	.0099	.0080	.0017	.0006	.0011	.0006

* Average of 4 species with densities closest to those of the contagious and regular species.

the quadrat size increases. It is of interest that the coefficient of dispersion is a linear function of the $\log_2$ of the quadrat size. In all cases, the $(D-d)/d^2$ measure gives the greatest differentiation, in that the maximum values for the contagious species are of the order of 100 times those for the random species, while the D/d values show five-fold differences or less. Whitford's $100D/F^2$ measure is intermediate in this respect and in addition is favored by ease of calculation, since it may be determined directly from the field data without recourse to tables or complex formulas.

For truly random species, K should equal unity (1.0) for D/d, $\Sigma D/\Sigma d$, and $V/\bar{x}$. According to Fracker and Brischle, $(D-d)/d^2$ should be from 0.0001 to 0.0030 for random distributions, while values above 0.02 indicate definite contagion. The same authors state that values for $V/\bar{x}$ less than 2.0 may be considered to indicate randomness, while values over 2.0 are typical of contagious distributions. Blackman ('42), however, set the limits of random distributions as measured by this coefficient as

$$1 \pm 2\sqrt{\frac{2n}{(n-1)^2}}$$

where n = number of sample quadrats. When suitable quadrat sizes are used, the $100D/F^2$ measure is about 0.024 for random species. Because of the great dependence of this test upon quadrat size, it should be used only with species of such density as to give frequencies above 20%. As can be seen in table VI, the values of K approach unity very closely for D/d, and $V/\bar{x}$ for the four random species whose mean areas most nearly approach those of the contagious and regular species. The minimum value of $100D/F^2$ was 0.029 while that of $(D-d)/d^2$ was 0.0006, thus agreeing very well with expectation. The average value of $\Sigma D/\Sigma d$ for all random species in the artificial population and for all quadrat sizes was $1.0486 \pm .019$ (St. Error).

The relation between frequency and density for random, contagious and regular species is shown in figure 14. As can be seen, frequency values are too low for any given density if the species is contagious and too high if the species is regular. Similar deviations are shown for the relation between frequency and constancy. On the other hand, density determinations are much more nearly accurate for the three types of dispersion, but there is some indication that highly contagious species are over-represented by relatively small quadrats. Further study is needed of the relationship between degree of contagion, quadrat size, and accuracy of density measurements. Frequencies and constancies thus increase with increasing quadrat size and decrease with increasing contagion. Presence values behave like constancies, although not with a predictable deviation. With fixed sample areas in any comparative study, the main factor affecting frequency and constancy values is the degree of non-randomness and both are lowered for contagious species. As a result most studies will give low values for these characters, since most species are contagious. It follows that relative frequencies for the dominant species are also low, since the lowering of the individual frequency values for these plentiful species will exert a greater effect on the percentage sum than will similar changes in the rare species.

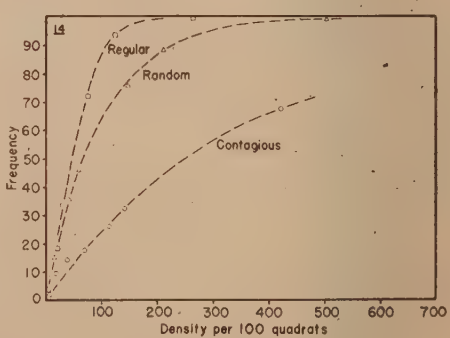

FIG. 14. The relation between frequency and density for species with regular, random and contagious dispersions. Data from artificial population.

Application to Actual Field Data

The application of these interrelations to actual field data is shown in the graphs accompanying this section. They are representative examples taken from the recent literature in American phytosociology, and are intended to show how the interrelations may be used to gain a better understanding of community structure.

Frequency-Density.—A large number of studies of the deciduous hardwood associations of eastern United States have been made in recent years. Many of the reports of these studies include tables of both frequency and density and most of these indicate that the trees are distributed at random, as shown by the close resemblance between actual and theoretical frequency-density curves. Cox Woods, a beech-maple woods in Indiana (Potzger, Friesner, and Keller '42), offers a good example of this agreement (fig. 15). All except a few of the least common species show densities close to those to be expected for a random distribution. The value of K for $\Sigma D/\Sigma d$ is 1.292 for this woods. On the other hand, a few studies apparently show marked non-agreement. This is illustrated (fig. 16) by Klein Woods, an oak-beech woods also in Indiana (Keller '46), where all species with frequencies greater than 40% show densities much greater than those to be expected by chance, with a $\Sigma D/\Sigma d$ value of 2.53. The rare species appear to be more nearly random in this instance. Another example of an assemblage with pronounced contagiousness is that of Warren's Woods, a beech-maple forest in Michigan (Cain '35) with a $\Sigma D/\Sigma d$ of 12.6. In these last two cases, trees of all sizes were included in the calculations. If trees over 1″ DBH only are used for Warren's Woods, then the agreement with random expectations is much better with a $\Sigma D/\Sigma d$ nearly equal to unity. This might indicate that the seedlings and small saplings are responsible for the apparent contagiousness of the species; they are evidently dependent upon small habitat variations for temporary establishment in numbers but are liberated to grow to maturity by chance factors which are not correlated with the habitat.

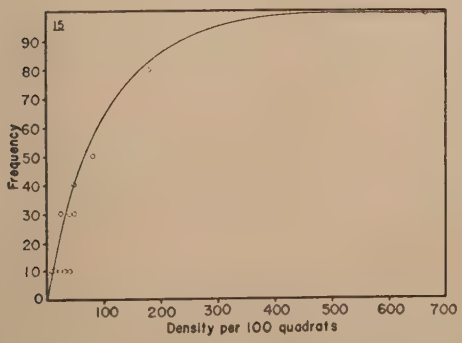

Fig. 15. The relation between frequency and density for trees in Cox Woods. Solid line indicates theoretical relation for random population. Data from Potzger, Friesner and Keller ('42).

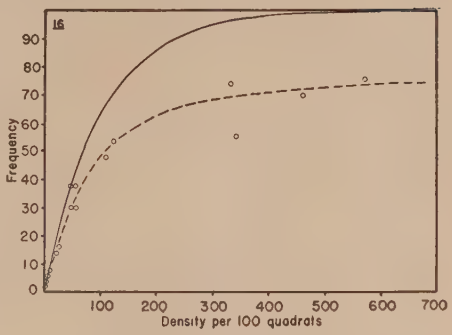

Fig. 16. The relation between frequency and density for trees in Klein Woods. Broken lines through actual data; solid line indicates theoretical relation. Data from Keller ('46).

Further support for this observation is to be found in the work of Eggler ('38) on the maple basswood forest of Hunt Hill Woods in Washburn County, Wisconsin. As shown in figure 17, trees from 1″ to 3″ DBH are relatively contagious, while the trees 10″ DBH and over are almost perfectly random.

Similar results are indicated by the data of several other forest ecologists, as summarized in table VII. Generally stated, the figures indicate that small seedlings are very contagious, samplings are more

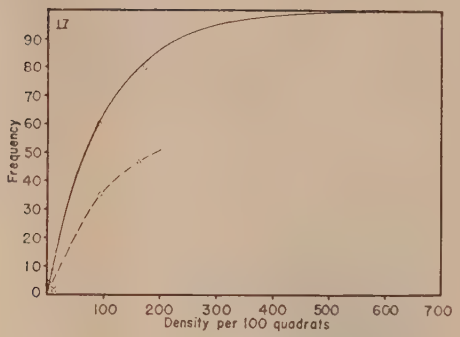

FIG. 17. The relation between frequency and density for trees of two size classes in Hunt Hill Woods. Triangles—trees from 1″ to 3″ DBH. Circles—trees 10″ DBH and over. Solid line indicates theoretical relation. Data from Eggler ('38).

nearly random, while the mature trees approach a truly random condition in the larger size classes. There is also some indication that the mature trees are more random in the self-reproducing climax forests than they are in the earlier stages of succession, thus supporting the contentions of Whitford ('49). It should be realized that at least a portion of this decrease in apparent randomness with increase in tree size is due to the low number of large trees which can possibly be present in the standard 10 × 10 M quadrats used in these investigations. Very high values of D/d cannot be obtained under these conditions.

Frequency-Constancy-Presence.—There are very few studies of American plant associations in which the data for both frequency and true constancy are given. In most investigations, constancy figures as given were not obtained from a single large sample per stand, but were calculated by the summation of data from a fixed number of smaller quadrats in each stand, usually 10 or 20 quadrats, each 100 square meters in area. Such figures are not truly valid constancy values, since any possible interaction between plants is eliminated by the scattered samples (Clapham '36). Figure 18 shows the results obtained by Lee ('45) for 20 stands in the White River flood plain of Indiana.

As can be seen, the constancy values are much too low for any given frequency, when compared to the expected random

TABLE VII. *Relative randomness* ($\Sigma D/\Sigma d$) *for trees in different size classes*

Investigator and forest type	Less than 1″ DBH		More than 1″ DBH		
	Less than 1′ high	More than 1′ high	1″–3″	4″–9″	10″ +
Eggler (1935) Maple-Basswood	5.68	2.50	2.26	1.20	1.05
Stearns (1949) Maple-Birch-Hemlock	3.10	—	—	—	1.02
Daubenmire (1935) Maple-Basswood	2.52	1.76	1.65	1.37	1.11
Anderson (1948) Maple-Birch-Hemlock	—	—	2.00	1.56	1.12
Wagner (1947) Oak-Basswood	4.55	2.66	2.36	1.48	1.19
Cottam (1949) Oak	5.87	2.76	2.00	1.32	1.32
Curtis (1947) Palo Verde	3.34	3.13	1.76	1.88	1.84
Average	4.176	2.562	2.005	1.468	1.235

numbers. This might be interpreted as contagiousness in the usual sense, but more probably it indicates that the several stands were not really isolated portions of a uniform assemblage, but rather represented slightly different combinations of species. The whole question of the delimitation of stands and the artificial nature of the boundaries of present day plant communities is involved here. In most agricultural regions, undisturbed stands of any natural vegetation type are surrounded by cultivated fields with the result that normal migrations are greatly impeded. Certain species may reach high population levels due to the chance absence of particular competitors from the stand at the time it was delimited from the main matrix of the association or due to their chance extermination at some later time. Study of frequency-constancy interrelations may often be of help in pointing out species which have "irrupted" in this way and thus aid in pointing out the direction to be taken by further research.

The relation of frequency, constancy and presence for plants of the alpine fell fields of Colorado (Cain '43) is shown in figure 19. This curve is typical of the few studies in which the necessary data

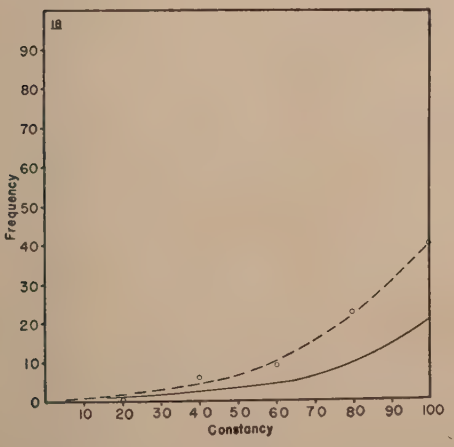

FIG. 18. The relation between frequency and constancy for trees in 20 stands in the White River flood plain of Indiana. Solid line indicates theoretical relation. Data from Lee ('45).

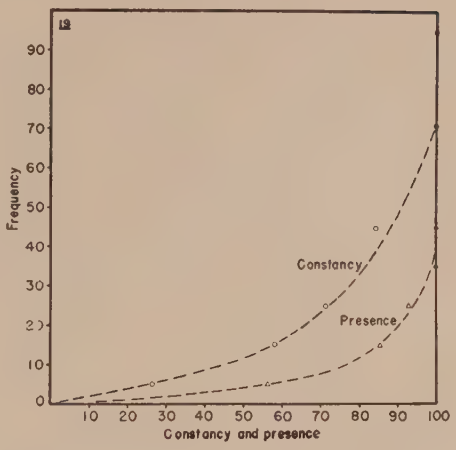

FIG. 19. The relations between frequency and constancy and presence for plants of the alpine fell fields of Colorado. Data from Cain ('43).

are presented. For any given frequency, the presence values are much higher than the constancy values. Since no standard sizes have been adopted for constancy determinations and since none are possible for presence studies, no fixed or theoretical set of curves can be given. On the basis of the data examined thus far, it would appear that presence values reach 100% when the frequencies reach about 40%, while constancy values reach 100% when the frequencies reach about 60%, but it should be emphasized that these are generalizations only. The shape of the curves and their end points are clearly controlled by the latitude of variation allowed by the investigator in his choice of stands for study. The more nearly similar are the several stands, the lower will be the constancy and presence curves, while the more different the stands, the higher the curves.

DISCUSSION

The interrelations between various phytosociological measures demonstrated in the preceding sections may be used in several ways in the study of plant communities. Perhaps their greatest use lies in

their ability to describe the nature of the dispersion of the component species. They are of lesser value in the problem of community delimitation. As Ashby ('36) has pointed out, statistics do little to remove the subjective judgments connected with delimitation. The individual ecologist must still make a personal estimate as to when and where his community starts and stops. Once he has done this, however, then the mathematical interrelations of the characters he determines may tell him much about the structure of the community. They are particularly valuable as indicators of the degree of non-randomness of the component species.

If the main species in an assemblage are randomly distributed, then certain conclusions are immediately in order. In the first place, such a chance distribution of individuals indicates that all factors of the environment are at or near their optimum point for these species; the habitat may be said to be uniform. Consequently, no further investigation is necessary beyond a description of the salient features of the environment. In addition, a random distribution of an abundant species indicates that it has reached a peak importance in the community and consequently must have been present for a considerable length of time (Whitford '49). In communities below the climax level it is also an indication that the species will decline in the near future. If the species are random, then only one or a few phytosociological characters need be studied to give an adequate picture, since the others may be deduced through the use of the interrelations.

If the main species show contagious distribution, then explanations become necessary. These explanations may be based on age of occupation of the site by the species, or, more usually, on the occurrence of a non-uniform habitat, with irregular distribution of local areas of differing environment. Full exploration of these possibilities may lead to a demonstration that more than one community is involved, or else may give valuable information concerning the age or successional status of a uniform community. In any case, the presence of such a distribution definitely indicates that extreme caution should be used in the interpretation of results. This is especially true when comparisons are to be made with the results of other investigators, who may or may not have been concerned with a similar, non-random distribution. It is necessary to present data on many or all characters for such assemblages, since there is no convenient way to predict one from the other.

In view of the above, it becomes apparent that the most important determination to be made in the detailed analysis of any community is the measure of randomness of the main species. The current study was not designed to find the best method of measuring randomness and consequently no concrete recommendations can be made. It would appear that Fracker and Brischle's index is most sensitive, while Whitford's measure is the easiest to calculate. Future statistical studies will no doubt clarify this problem further and provide us with other and better techniques.

The extreme importance of quadrat size emphasizes the need for careful choice of sample area in the study of any given plant community. If the quadrats are too large, then frequency values in the 80% to 100% class will be numerous. Such values are of low usefulness, since the shape of the interrelation curves is such that minimum accuracy will obtain in the prediction of the magnitude of other characters, such as density, abundance, constancy and presence. It would appear that a suitable size of quadrat is one which is equal to the mean area of the species with greatest number of individuals. If random, such a species would have a frequency of 63% and all others would have lesser frequencies. The densities of all species would show a nearly linear relation to frequency, since the frequency-density curve is nearly straight in this region. Most species would have con-

stancy values less that 100%, while only a few presence values would reach that figure. On the other hand, such values as relative frequency attain their maximum usefulness when the quadrat is four times the mean area of the most numerous species. It would appear, therefore, that a practicable compromise could be attained by the use of a quadrat which was twice as large as the mean area of this most common species. All random species in this case would have frequencies of 86% or less.

The absolute size of such a quadrat would be slightly different for each community, and hence the results of several studies could be compared only with great difficulty. In practice, it appears that each of the major plant formations or their synusia have a rather limited range in mean areas of their dominant plants, and therefore may be studied by means of certain standardized sample sizes. For example, in the eastern deciduous forest of North America, the trees are so spaced that a quadrat 10 meters on edge will give frequency values less than 100% for all species in nearly all cases, but will show a few species with values above 80%. Under such conditions, maximum information can be readily obtained. The shrubs seem to be adequately sampled by quadrats 4 meters on edge, while the herbs seem best examined by quadrats one meter square. In the last two cases, there have been insufficient studies to date to be certain that the indicated sizes are actually optimum. Further study should be given the problem, so that standardized sizes may be agreed upon at the earliest possible date. Results from such standardized quadrats would be instantly comparable as between different investigators, at least as concerns random species, which is a situation far different from that existing today. Suitable sizes for other formations can be worked out from existing data or from future studies designed for the purpose.

Summary

1. This study is concerned with the mathematical interrelations of certain phytosociological characters (frequency, density, mean area, abundance, constancy, and presence) as determined by sampling an artificial population constructed on the log-normal basis suggested by Preston ('48), and with the effect of quadrat size and degree of randomness of the species on these interrelations.

2. The basic characters are defined by the following formulas:

$$\text{Frequency } (=F) = \frac{\text{No. of quadrats in which a species occurs}}{\text{Total no. of quadrats examined}} \times 100$$

$$\text{Density } (=D) = \frac{\text{Total no. of individuals of a species found}}{\text{Total area examined}}$$

$$\text{Mean area } (=M) = 1/D$$

$$\text{Abundance } (=A) = 100D/F$$

$$\text{Constancy } (=C) = \frac{\text{No. of samples (one per stand) in which a species occurs}}{\text{Total no. of stands examined}} \times 100$$

$$\text{Presence } (=P) = \frac{\text{No. of stands in which a species occurs}}{\text{Total no. of stands examined}} \times 100$$

3. The artificial population consisted of 33 species, with numbers of individuals varying from two to 1,600. There were more species with intermediate numbers of individuals than species with either very few or very many. The majority (30) of the species were distributed at random. Two of the species were arranged in clusters, while one species was given a perfectly regular spacing. The quadrats used varied in size from one half

the mean area of the most plentiful species to 100 times larger than that area.

4. The relation between frequency and density given by the formula, $F = 100 (1 - e^{-D})$, was closely approximated by all random species at all quadrat sizes. The interrelations between quadrat size, density, mean area and frequency may be represented by a straight line (fig. 7).

5. The quadrat size which gave, on the average, 50% of the total number of species in the population was equal to ½ the mean area of the species with the modal number of individuals.

6. An interpretation is given to Raunkiaer's "normal" curve of distribution of frequencies which indicates that species in the 1–20% frequency class have mean areas over 4 times that of the quadrat used while species in the 81–100% class have mean areas less than one half the size of the quadrat. It is considered that the distribution curve is of no value as a measure of homogeneity.

7. The agreement between theoretical values and actual values as determined on the random species of the artificial population was good for the frequency-relative density interrelations.

8. Study of the non-random species showed that the measures of randomness proposed by McGinnies, Clapham, Fracker and Brischle, and Whitford are all dependent upon quadrat size, with some showing an optimum relation between mean area and quadrat size while others changed progressively with changing quadrat size. It is considered that Fracker and Brischle's method is the most sensitive, while Whitford's is the easiest to use.

9. For any given quadrat size, frequency and constancy values are decreased for contagious species and increased for regular species as compared with random species. Frequency, density, constancy and presence values are increased with increasing quadrat size for any degree of dispersion but the increase is least with contagious species and greatest for regular species.

10. Application of these interrelations to actual field data mostly obtained in forest communities showed that mature trees tended to be randomly distributed particularly in the larger size classes, while the smaller trees were more contagious, with maximum contagion exhibited by the seedlings and small saplings.

11. It is concluded that a practicable size for the study quadrat is one which will give frequencies of less than 86% for all random or contagious species. Ordinarily, this will be a quadrat which is twice as large as the mean area of the most numerous species. Such a quadrat will give maximum information about all of the important species of the community.

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RELATION OF MERRIAM KANGAROO RATS TO RANGE VEGETATION IN SOUTHERN ARIZONA[1]

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Livestock grazing practices and climatic variations are known to affect the character and abundance of range vegetation. Fluctuations in kinds and numbers of small mammals often accompany these vegetal changes. Certain animal species increase while others decrease as vegetation retrogresses from climax conditions (Phillips, '36). Ground squirrel populations are smaller on ranges protected from livestock grazing (Linsdale, '46). Some animal communities even seem to be dependent upon vegetation remaining at a sub-climax level (Taylor *et al.*, '35).

In some instances, small mammal populations are suspected of affecting floristic composition. Arnold ('42) suggests that a range may be held in a lower successional stage of vegetation, once that level is reached, by the presence of small native herbivores alone. Bond ('45) expresses the opinion that recovery of desired range vegetation might be enhanced by the differential feeding pressure of certain rodents.

This study concerns the effect of the behavior and abundance of Merriam kangaroo rat (*Dipodomys merriami merriami* Mearns) upon the character and condition of range vegetation.

AREA AND PROCEDURES

Field work was conducted on the Santa Rita Experimental Range which is maintained by the Southwestern Forest and Range Experiment Station, U. S. Forest Service, about 30 miles south of Tucson, Arizona. Studies were confined to the mesquite (*Prosopis juliflora*)—burroweed (*Applopappus tenuisectus*) community, between 3,000 feet and about 4,200 feet elevation, which has replaced the former semidesert grassland aspect made up of mixed perennial grasses and minor amounts of shrubs and herbs. There are two growing seasons in this region; one results from winter showers, and the other from heavy summer precipitation during July and August. In years with favorable precipitation, many species of annual grasses and forbs mature during the spring months, and the summer rainy season is characterized by the maturation of perennial grasses and numerous annual plants.

The Merriam kangaroo rat is a small rodent of nocturnal habit common to the area of study. These animals are widely distributed, easy to trap, and reach such population levels as to make significant sampling possible. Seeds from many species of vegetation furnish the main food items.

Other small rodents occupy the same vegetative type as the Merriam rat. Among these are the Bailey pocket mouse (*Perognathus baileyi baileyi* Merriam), the Price pocket mouse (*P. pencillatus pricei* (Allen)), grasshopper mice (*Onychomys* spp.), white-footed mice (*Peromyscus* spp.), the white-throated woodrat (*Neotoma albigula albigula* Hartley) and the bannertailed kangaroo rat (*Dipodomys spectabilis* subsp.). Diurnal rodents in-

[1] This work was conducted while the author was a member of the Botany and Range Ecology Department of the University of Arizona. Within this department, Horace S. Haskell did a large share of the field work, and Robert A. Darrow assisted with plant identifications. The work was done on the Santa Rita Experimental Range in cooperation with the Southwestern Forest and Range Experiment Station, U. S. Forest Service. A. Starker Leopold of the University of California critically read the manuscript. Live traps for the study were furnished by the U. S. Fish and Wildlife Service.

clude the roundtailed ground squirrel (*Citellus tereticaudus neglectus* (Merriam)) and the Harris ground squirrel (*C. harrisi harrisi* (Audubon and Bachman)). The Merriam kangaroo rat probably equals in abundance the white-throated woodrat (Vorhies and Taylor, '40) and the bannertailed kangaroo rat (Culley, '39), and is much more numerous than ground squirrels and pocket mice. Grasshopper mice and white-footed mice are rare on the Experimental Range. Since most of these rodents live on material other than seed, or if subsisting on seed are of limited abundance, it is felt that the Merriam rat exerts the primary influence with regard to destruction and dissemination of seeds.

Exclosures on the Experimental Range protected from grazing for 15 to 30 years, presented a wide selection of perennial grass conditions. The exclosures (two or more acres in size) were large enough to have characteristic small rodent populations of their own. Populations of kangaroo rats were sampled on paired quadrats inside and outside of five such selected exclosures during the summer of 1946. The trapping quadrats were one-half acre in size and contained fifty traps of the museum breakback type. Traps were set and baited with rolled barley each night for three consecutive nights. Rodent numbers were expressed on a per acre basis, according to the border equivalent correction method advocated by Dice ('38).

Food plant availability was determined on several "representative" plots at monthly intervals to gain some idea of food preferences of rats in relation to plant abundance. Relative abundance of plant species was computed by dividing total number of plants for an individual species by total numbers for all species. Density of perennial grass was measured by the line interception method (Canfield, '41).

Rodent Numbers in Relation to Perennial Grass Density

Table 1 compares rodent numbers and perennial grass densities on grazed and adjacent protected areas. Greater numbers of rodents were consistently taken on the grazed areas outside of the exclosures. Perennial grass density was consistently as great or greater inside the exclosures. Average comparisons for all exclosures were: For kangaroo rats, 2.0 anmials per acre inside, 7.4 outside; for perennial grass density, 0.9 per cent inside, and 0.4 per cent outside.

To determine the character of the relation between Merriam rat numbers and abundance of perennial grass, a graphic comparison was made. This comparison was confined to mature animals to eliminate the effect of increasing numbers of immature animals which were captured as the breeding season progressed. A parabolic curve, fitted by the method of least squares (Snedecor, '40), proved better than a linear regression for representing the data (figure 1). This graph indicates that an increase in perennial grass abundance is accompanied by a decrease in kangaroo rat numbers.

While kangaroo rats were in greater

Table 1. *Number of Merriam kangaroo rats per acre compared with density of perennial grass on protected and adjacent grazed areas*

Plot No.	Grazing treatment	Perennial grass density (per cent)	Number of Merriam rats per acre	
			Mature	Immature
I	Protected	1.6	0	0
	Grazed	0.5	3.6	0.7
II	Protected	0.4	1.6	0
	Grazed	0.4	3.3	0
III	Protected	0.6	3.6	0.7
	Grazed	0.05	8.7	10.0
IV	Protected	1.5	1.1	0.7
	Grazed	0.5	3.5	1.8
V	Protected	1.1	2.2	0
	Grazed	0.7	4.6	0.7

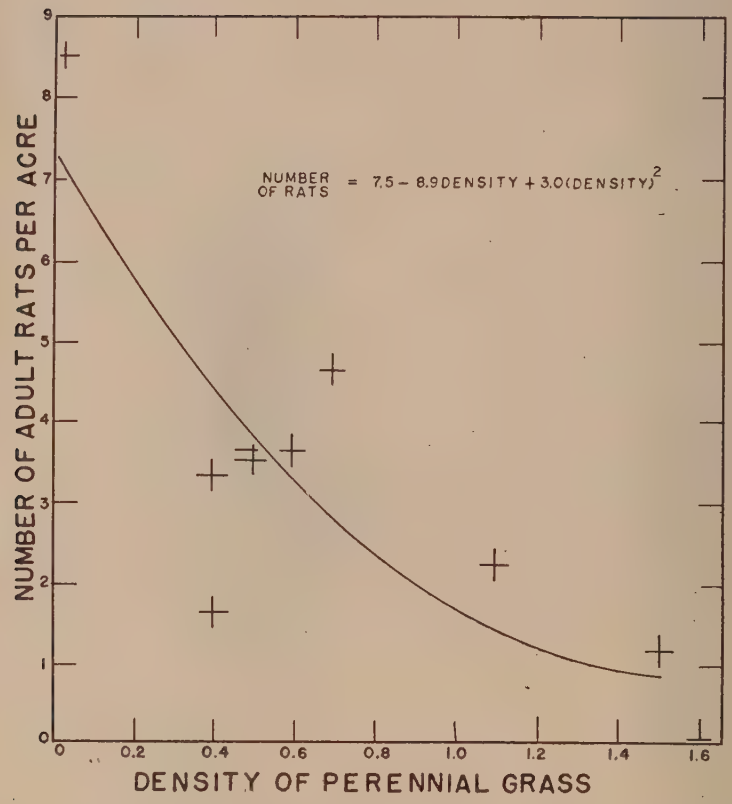

FIG. 1. Relation between perennial grass density and number of Merriam kangaroo rats per acre.

abundance on areas of lesser grass density, these animals cannot be held directly responsible for grass decline. Rats had free access to the protected areas but were in lesser numbers, and grass density was higher thereon. Other factors must have been responsible for the decrease in grass. Merriam rats appear merely to prefer the habitat afforded by lower grass density.

The factors responsible for the preference shown by rats for a habitat of lower grass density are not known quantitatively. However, the relation of grass abundance to the mode of escape used by these rodents is probably a major factor. When released from live traps these animals employ a speedy and zig-zag run in returning to their burrows. Perhaps the same procedure is followed in evading aerial and terrestrial predators. If so, such an escape mechanism would be hampered as perennial grass abundance increased, inasmuch as a fast retreat along the ground would become more difficult.

FOOD HABITS IN RELATION TO VEGETATION

Table 2 summarizes the preference of Merriam kangaroo rats for plant items identified in the pouches of 292 animals.

Food preferences.—Seeds dominated cheek pouch contents almost to the exclusion of other plant items. Only rarely were leaves or stems of a plant found. Stomachs sometimes contained green ma-

terial—mostly during periods of new vegetative growth in spring and summer. Seed stalks were clipped at times. Vegetative destruction other than seeds is so limited, however, as to produce little effect upon floristic composition or herbage production.

Grass seeds comprised the bulk of the material in the pouches. Forb seeds were second in abundance and woody plants third. Annual grass seed was recovered more than twice as frequently as perennial grass or forb seed. Mesquite and cactus seed occurred least frequently in pouches.

To obtain an arbitrary "use rating," percentage abundance of total vegetation (number of plants per unit area) was divided by percentage occurrence of plant items occurring in cheek pouches (table 2). Admittedly, this comparison assumes that an equal number of seeds are produced by different species. However, the comparison is believed to be roughly indicative of whether a plant item is actually preferred, or whether availability is more important in influencing food selection. On this basis, mesquite and cactus seeds have outstanding "use ratings," and presumably are preferred food items. Perennial grass seed also appears to be taken in greater amounts than would be expected on the basis of its availability. Accordingly, the greatest influence of these animals on range vegetation would thus be expected to be in relation to perennial grasses and shrubs.

TABLE 2. *Major plant items recovered in Merriam kangaroo rat pouches compared with plant abundance*

Plant group	Percentage of occurrence in pouches	Percentage of total vegetation	Use rating
Grasses			
Annual	69	35	2.0
Perennial	33	5	6.6
Forbs			
Annual	34	39	0.9
Perennial	34	15	2.3
Woody			
Mesquite	9	0.3	30.0
Cacti	13	0.5	26.0
Other	4	5	0.8
Unidentified	7	—	—

TABLE 3. *Seed selection by Merriam kangaroo rats in relation to seed size and plant stature*

Plant group	Per cent of pouches containing			
	Large seeds*		Small seeds	
	Tall plants†	Short plants	Tall plants	Short plants
Grass				
Perennial	32	—	3	—
Annual	—	64	14	—
Forbs				
Perennial	2	33	—	—
Annual	—	2	—	88
Woody				
Shrubs	13	—	—	—
Cacti	13	—	—	—

* Less than 500,000 seeds per pound.
† Always more than 6 inches in height.

Plant characteristics affect food selection.—Food selection is influenced by both size of seed and stature of plants (table 3). Large seeds occurred most frequently in pouches, whereas the small seeds that were recovered belonged to plants of low stature. Most of this smaller seed was harvested directly from the plants before the fruits dehisced. Some of the larger seed on low growing plants was also collected in this way. Seed of large-seeded perennial grasses and shrubs was picked up for the most part from the ground. Apparently, larger seed may be recovered either before or after seed is cast, but small seed must be harvested directly from plants during the period of seeding.

Relation of Food Habits to Perennial Grass and Shrub Establishment

Records kept by Robert A. Darrow[2] from 1931 to 1946 on certain exclosures open and closed to rodent grazing made possible a comparison of the influence of kangaroo rats on establishment of perennial grasses, mesquite, and cacti—the preferred food items of these rodents.

[2] Unpublished manuscript.

Perennial grass.—Perennial grasses were divided into two groups—those with large seeds and those with small. Black grama (*Bouteloua eriopoda*) and Rothrock grama (*B. rothrocki*) were the main small-seeded plants. Threeawns (*Aristida* spp.), cottongrass (*Trichachne californica*), and tanglehead (*Heteropogon contortus*) were the most common large-seeded species. Seeds of the large-seeded plants occurred abundantly in cheek pouches, while seeds of the smaller-sized perennials were seldom if ever found.

Figure 2 shows the changes in relative abundance of perennial grass and shrubs which occurred between 1931 and 1946. Small-seeded perennials were unaffected by the presence of rodents. This class of perennials has yet to return to the abundance which existed at the start of the study.

Large-seeded perennials are apparently

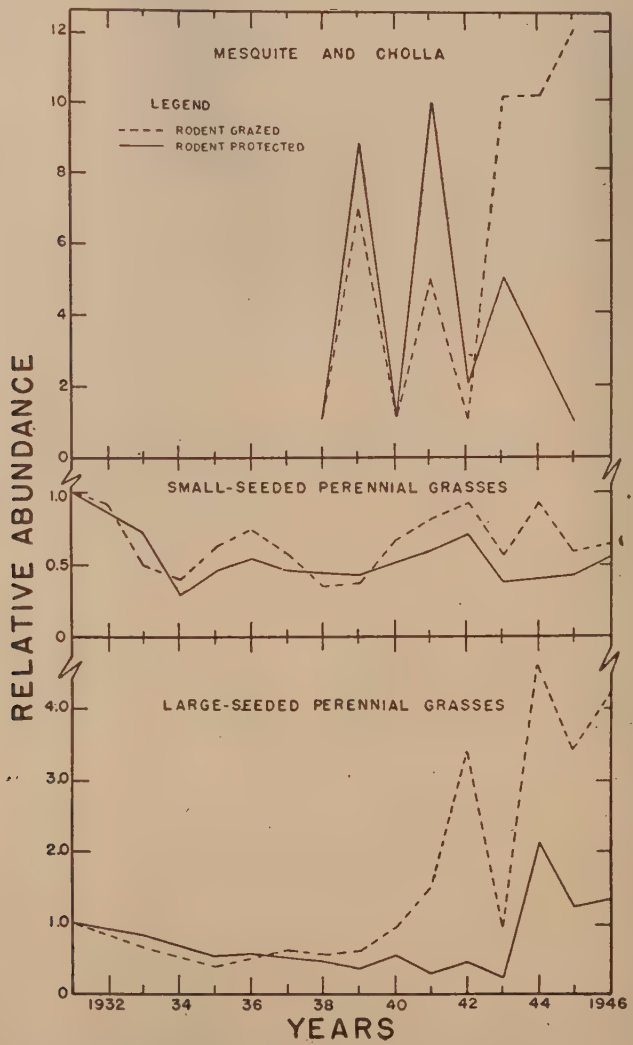

FIG. 2. Relative change in abundance of certain plants on rodent grazed and rodent protected areas from 1931 to 1946.

related to rodent activity. Shortly after measurements of vegetative abundance were commenced, drought caused serious losses among these plants. During this period of low seed production, the rodent grazed area deteriorated faster than the rodent protected area. A large portion of the seed produced during this period was probably consumed by rodents. Under more favorable climatic influences after 1936, the experimental plots began to recover. Vegetation upon the rodent grazed plots then recovered more rapidly than upon ungrazed areas.

The faster recovery of large-seeded perennial grasses on rodent grazed areas might be explained as follows: Merriam rats harvest large volumes of seed during the time of seed availability. Uneaten seed is stored in small caches in the surface soil. During the late fall and winter months many of these caches are reopened. During a favorable seed year, much more seed is doubtless stored in the soil than is ever recovered. The seed which is left in the ground is in a more favorable environment for germination and early seedling survival than seed merely lying on top of the ground. Thus, when seed is plentiful and range plants are increasing in abundance because of favorable climatic influences, rate of plant restocking may be enhanced by the presence of Merriam rats.

Mesquite and cholla.—The same relation outlined above for large-seeded perennial grass also holds for mesquite and cholla, although the data are not so striking. The seeds of these plants occurred quite commonly in pouch contents (table 2). From 1931 to 1937, few seedlings of these plants survived on the charted enclosures. After 1938, seedlings of both species began to appear and the rodent grazed plots showed a more noteworthy establishment of seedlings.

Relation to Range Improvement

The reciprocal relation of the Merriam rat with range vegetation has a bearing upon the attitude to be taken toward this rodent in range management activities if the potentials of an area are to be fully utilized for livestock production.

Reseeding.—Forage plants which will be principally affected by Merriam kangaroo rats are those depending upon seed for reproduction. Moreover, only those plants which have relatively large seeds —fewer than 500,000 seeds per pound— will be appreciably influenced.

Ranges having a low density of perennial grass, as a result of improper management or inclement climate, will suffer the most detriment. Rodent feeding pressure on such areas may be sufficient to prevent plant reproduction.

During poor seed years, the effect of Merriam rats will be relatively greater. Where rodents are abundant, their food requirements may not be met during an unfavorable seed year. All seed stored in the surface soil will probably be recovered and consumed. During good seed years, the reverse could be expected, and rodent activity may result in placing more seed in a favorable environment for germination.

The influence of Merriam kangaroo rats upon artificial reseeding practices will depend mainly upon the size of seed being used. Seed as small or smaller than black grama (500,000 seeds per pound) is not likely to be discovered and destroyed after planting. Larger seeds may be subject to considerable destruction. Experimental plantings of vetch (*Vicia* spp.) often have been completely destroyed because of excavation of the seed by Merriam rats. Seed as large as mesquite can be discovered and excavated by rats when planted as deep as two inches.

Range condition.—There is a rough correlation between density of range vegetation over a series of years, and range condition. Higher grass densities are associated with better range conditions. Since Merriam rats increase with a decrease in grass density the effect of these animals would become progressively greater as range condition becomes poorer. Conversely, as a range passes a certain

stage of recovery, the influence of Merriam rats may become beneficial because of their seed storing propensities. Beyond a certain stage of range recovery, the effect of these rodents is probably reduced to a negligible quantity.

Two major factors operate to make the habitat less favorable for Merriam rats as range condition improves. Large-seeded vegetation, the preferred food, is largely replaced by small-seeded plants because increasing perennial grass density forces out weedy annuals, and a change in the composition of the perennial grass mixture toward a greater proportion of small-seeded species occurs. Secondly, the increasing abundance of perennial grass could conceivably produce a physical obstacle to the escape mechanism of these animals.

Associated with a decrease in perennial grass density is the observed increase of mesquite, and cholla. The activities of Merriam rats probably favor such an increase. Poor range condition is apparently in this case compounded by rodent activity.

Rodent reductions.—Reduction of Merriam kangaroo rats may be a necessary step in restoring certain depleted desert ranges. Rodent removal, however, must be accompanied by adequate grazing control. Unless the habitat is altered by improved perennial grass conditions, these rodents will return to their former abundance in a short time. Poisoning results only in temporary reductions. Permanent reductions can be accomplished only by increasing the density of perennial grass cover.

Reduction of Merriam rat populations for purposes of increasing forage supplies appears to be justified biologically only where the density of perennial grass is low and can be increased by grazing management or range improvement practices; or where artificial reseeding is being attempted with large-seeded plants. The best time for control of this rodent to affect natural range improvement would be the early winter of a good seed year. Much seed would by that time have been stored by rodents in the surface soil. A favorable year for seed germination and plant survival followed by proper grazing management, would enhance the chances of inproving range condition.

Summary

1. Greater numbers of Merriam kangaroo rats were captured on grazed areas than on exclosures protected from livestock grazing for several years. Rat numbers tended to decrease as perennial grass density increased.

2. Annual grass seed occurred most frequently in cheek pouch contents; perennial grass and forb seed ranked next in abundance, and seeds of woody plants, last. Perennial grass, mesquite, and cactus seed seemed to be preferred because of larger size. Seed of these plants was gathered entirely from the ground, whereas seed of other species was often harvested directly from the plant. Minute seeds were nearly always taken in whole fruits.

3. Large-seeded perennial grass abundance on livestock protected exclosures was influenced unfavorably by kangaroo rats during periods of low seed production, but favorably during periods when abundant seed was available. These rodents also appear to contribute to the spread of mesquite and cholla.

4. The detrimental effect of Merriam rats will probably be most pronounced on ranges in poor condition where the density of large-seeded perennial grasses is so low that most of the seed is consumed. These animals may also be a nuisance where artificial reseeding with large-seeded plants is being attempted.

5. Reduction of kangaroo rats might be desirable under the above conditions. Control of rodents only enhances the possibility of seed germination. Livestock control must be practiced to assist in plant survival.

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NOTES AND COMMENT

OUTLINE FOR AN ECOLOGICAL LIFE HISTORY OF A BIRD, BASED UPON THE SONG TANAGER *RAMPHOCELUS PASSERINII COSTARICENSIS*

Introduction

Throughout the Caribbean lowlands of Central America, from western Panama into southern Mexico, one of the first birds to draw the attention of the traveller is a tanager of medium size, attired in velvety black plumage with an intensely scarlet rump. This is the male Scarlet-rumped Black Tanager. *Ramphocelus p. passerinii.* The female is a bird of very different appearance, clad in nondescript shades of brown, gray and yellowish-olive. This tanager is confined to clearings in regions where the natural vegetation is rain-forest; it often nests in door-yard shrubbery as well as in the tangled vegetation of neglected pastures and in abandoned fields once cultivated. In the Pacific lowlands of Central America typical rain-forest is the dominant vegetation only in southern Costa Rica and adjacent parts of the Republic of Panama. Here, separated by the high Cordillera from the Caribbean slope, occurs a very distinct race of the same species, *R. passerinii costaricensis.* The males, strangely enough, are not separable by appearance from those of the nominate race; but the females are distinguishable at a glance by their brighter plumage, with the chest and rump ochraceous or even orange, instead of pale yellowish as in the eastern form. In suitable habitats this western variety is no less common than its relative across the Cordillera; it is the most abundant of the birds which nest in my yard in the Térraba Valley of Costa Rica. Here it is resident throughout the year, and comes regularly to eat bananas at my feeding-shelf. The males have a pleasant although not brilliant song; in my experience they sing far more persistently than the birds of the nominate race. Indeed, they produce more music than any other passerine bird in the neighborhood, with the possible exception of Gray's Thrush, *Turdus grayi.* This is the more surprising when one recalls that the multitudinous species of tanagers in tropical America are more renowned for their amazingly varied plumage than for their musical ability, and that this is a non-territorial species. Hence I call it familiarly the "Song Tanager," although technically perhaps the designation of the western race should be "Pacific Scarlet-rumped Black Tanager."

The Pacific slope of southern Costa Rica is a region of heavy rainfall. From April or May until December showers, often torrential, fall almost every afternoon or evening. The single annual dry season is shorter and less pronounced than farther north, extending usually from early or mid-January to early or late March, and varying a good deal in length and severity from year to year. The Song Tanagers begin to nest with the return of the rains in March, starting early when these come early, late when the dry season is prolonged. Although with migratory birds in the North the males as a rule begin to sing before the females arrive and long before they start to nest, with the Song Tanagers males become songful at about the same time that females begin to build. The loose flocks, in which males outnumber females, persist throughout the nesting season; territories are not chosen and defended; fighting has never been observed. The birds are not colonial, however; nests are well scattered through suitable habitats; yet occasionally two or even three occupied nests will be found within a few yards; and once two active nests were separated by only four inches. The female builds without help, although often a male accompanies her and sings while she works.

The two eggs, pale blue blotched and spotted with black and shades of brown, are laid early on consecutive mornings; very rarely (in possibly one or two nests per hundred) there are true sets of three eggs; and with equal rarity two females lay in the same nest. The female alone incubates, hatching the eggs in 12 days and a few hours, rarely as long as 13 days. The male usually begins to help his mate feed the nestlings a few hours after they hatch, but is scarcely ever quite as assiduous in this occupation as the female. At some nests a male was never seen in attendance, a circumstance which suggests that polygamy sometimes occurs, as indeed is to be expected from the preponderance of females. The nestlings, unless frightened, remain in the nest between 12 and 13 days or sometimes longer, then depart spontaneously with no parental persuasion. Already well clothed with plumage, they go into hiding in low dense vegetation until their tails are grown and they fly well. They are fed for some weeks after leaving the nest, chiefly by their mother. Young males begin to acquire the brilliant adult dress soon after attaining full size, and when a few months old quite resemble the mature birds. Two broods may be reared in a season. By the end of June most birds have finished breeding for the year; but a few belated nests are found in August, exceptionally in September.

The following outline, although based upon the writer's experience with the Song Tanager,

has been extended so that it might serve as a guide for the study of other land birds, chiefly by the inclusion of sections on migration and territory, neither of which applies strictly to this species. Although it suggests observations more varied and more prolonged in years than most workers will be able to undertake, what one can accomplish with any species of bird varies enormously with its habits—whether it is shy or confiding, whether nests are easy or hard to discover and reach, whether it is readily trapped and banded—no less than with the time and energy of the investigator. Most of the questions here suggested were actually studied in detail for a single species by Mrs. Margaret M. Nice; the results are presented in her monumental "Studies in the Life history of the Song Sparrow."

Outline of Study

I. *Range and climatic requirements*
- A. General geographical distribution
  1. Physiographic barriers to dispersal
- B. Altitudinal limits
  1. Do these vary in different portions of the range, as between north and south?
- C. Migration
  1. Does the bird inhabit the same portions of its range at all seasons?
- D. Climate
  1. Mean annual temperature in the warmest part of the range and in the coldest
  2. Mean annual rainfall in the wettest part of the range and in the driest
  3. Annual march of temperature in a typical part of the range, or in the locality where the bird was most studied
  4. Annual march of rainfall and humidity as in (3)
  5. What climatic features appear to limit the bird's range in area and altitude? (If the species is migratory, breeding and wintering areas should be considered separately. See also VIII E 3.)
- E. Relation to cognate forms
  1. What relation does this bird's range bear to that of congeneric or conspecific forms that might compete with it?
  2. That might interbreed with it and cause it to lose distinctness?

II. *Habitat*
- A. Vegetational types which the bird frequents
  1. List the dominant species of plants
  2. Does the bird use different types of vegetation for feeding, for nesting, for roosting, for refuge?
  3. Is the bird restricted to particular levels within the vegetational association(s) it frequents?
  4. What causes the bird to avoid certain types or levels of vegetation within its range? (In tropical regions the restriction of birds to vegetational formations is often striking. A bird of the clearings may never be seen a hundred yards within the neighboring forest, and some of the forest-dwellers seem never to venture into the clearings. Very little is known of the physiology or psychology underlying this restriction. A study of microclimates might be illuminating.)
- B. Associated species of birds
  1. List the principal avian associates
  2. What are the bird's relations with the non-predatory species with which it normally associates?
  3. How does it react to a harmless strange bird, e.g. a straggler from a neighboring plant formation which it avoids?

III. *Food*
- A. Principal food plants and their seasons of bearing
- B. Principal insects and other animals eaten and their seasonal occurrence
- C. Special food requirements (if any) of the young
- D. Relation of the season of reproduction to the annual fluctuations in the kind and abundance of available food (see also VIII D 3)
- E. Methods of capturing or gathering animal and vegetable foods

IV. *Structure and plumage*
- A. Consider bill, feet and other structures in relation to the bird's food and manner of foraging
- B. Consider the length of the bird's wings in relation to its migratory or sedentary habit
- C. Other structural modifications of ecological significance
- D. Coloration
  1. Does the bird's plumage blend with the background?
  2. How is the diverse coloration of the sexes related to their participation in the activities of the nest?

V. *Social habits*
- A. During the non-breeding season
  1. Does the bird live solitary, in pairs or in flocks?
     a. If in flocks, of what range in size?
     b. Is there segregation of sexes and ages?
     c. Is there a "leader"?
     d. Do some members of the group "dominate" others?
  2. If the bird forages in mixed flocks, what are its associates and how do they interact?
  3. Does the bird roost alone or in company?
  4. What means does the bird employ to maintain contact with its mate or companions?
- B. During the nesting-season

1. Is the bird solitary or gregarious during the breeding-season?
2. If it claims a territory, what are its relations with its neighbors (see also IX A 2)?
3. If sexually immature grown birds, or mature but mateless birds, are present during the nesting-season, what are their relations with the breeding birds?

C. On migration
1. Does the bird migrate singly, in flocks of its own kind, or in mixed flocks?
2. Is there segregation of sexes or ages on migrations? Do males precede females? Do young precede old?

VI. *Enemies and hazards*
A. List the known avian, mammalian and other animal predators of the adults. If possible, indicate frequency of predation by each
B. The bird's reactions to the approach of potential enemies
1. Notes used to warn of approach of (a) aërial, (b) terrestrial enemies
2. Mode of taking refuge from (a) aërial, (b) terrestrial enemies
C. Effects of adverse weather—storms, hurricanes, protracted rains, drought, etc.
D. Effects of human activities—hunting and malicious persecution, agricultural operations, forest or brush fires, buildings, traffic, etc.
1. Are human activities on the whole beneficial or deleterious to the species?
E. Is the bird subject to diseases?
F. What external and internal parasites are known?
G. Predation on nests (see IX H 1)

VII. *Diurnal rhythm*
A. Time of beginning day's activities
1. Relation of time of arising to light intensity
2. Variations with weather
3. Do males or females become active first?
B. Are special periods of the day devoted to foraging and resting? To singing? To nest-building?
C. Does the bird divide its day between various parts of its habitat in a more or less methodical fashion?
D. Manner of taking shelter from rain and storms. Does a light rain inhibit feeding? A torrential rain?
E. Time of retiring to roost, as related to light-intensity, weather and sex

VIII. *Annual cycle*
A. Plumage
1. How many molts are there in a year? At what seasons? Are they partial or complete?
2. Are there seasonal changes in coloration of males? Of females? Are these effected through molting, plumage-wear, or by other means?
3. How are the molts related to the annual march of temperature and rainfall?
4. If changes in coloration occur, how are they related to changes in the vegetation?

B. Weight (If birds are trapped and banded it will be well worth while to weight them.)
1. Are there daily rhythms in the weights of the birds? (It will be necessary to know this before fluctuations over longer periods can be studied.)
2. Are there annual fluctuations in the weights of adult males? Of adult females?
3. Can these fluctuations be correlated with:
a. Migratory or non-migratory habit?
b. With annual curve of temperature or precipitation?
c. With variations in available food?
d. With reproductive activities?

C. Song
1. Do both sexes sing?
2. Is singing seasonal or does it occur throughout the year?
3. What are the factors which influence the inception and decline of song, or its fluctuations in volume, if these occur?

D. Nesting
1. In what months does the bird nest? (When sufficient information is available, it should be presented in a graph or table, showing the distribution of nests by months. Each nest should be entered under the month when the eggs were laid, as observed or calculated from subsequent study.)
2. Can the nesting-season be correlated with the annual curve of temperature, of rainfall, or other meteorological conditions? How is it related to variations in the quantity or quality of available food?
3. How does the date of the inception of nesting (or of maximum nesting) vary from year to year with variations in weather, or in abundance of food?

E. Migration
1. Trace the chief migratory movements, with dates of arrival and departure at various points
2. Where possible, distinguish times of arrival of males and females, old and young
3. Attempt to correlate these movements with external conditions as in VIII D 2 and 3

IX. *Reproductive activities*
A. Territory (Does the bird select for purposes of nesting an area from which it attempts to exclude others of its kind?)
1. Character of the territory
a. Is the defended area merely a nest-site, or does it include sources of food?

b. What must the territory contain in the way of trees or other sites for singing and for nests? Of vegetation for refuge? Of sources of food? Of water?
c. Range in size of territories
2. Selection and defense of the territory
a. Is the territory chosen by the male or both sexes together?
b. How do the birds announce the possession of territory?
c. How do they react toward invaders of their own species? Is there any distinction in the treatment of male and female trespassers? Do the owners of both sexes defend the territory against invaders of both sexes?
d. How do the birds behave when birds of other species, or animals of other kinds, enter their territory?
3. Period of tenure
a. How long before the inception of nest-building is the territory claimed?
b. Is the defense of the territory relaxed after incubation has begun? After the young hatch? After they leave the nest?

B. Relations between the sexes
1. Is the bird monogamous, polygamous, or otherwise?
2. How long does the bond between mates endure?

C. Nest-site
1. Which sex selects the nest-site?
2. Character of the nest-site
a. Kinds of trees, bushes, etc., that may be chosen
b. Height above ground (Give extremes and average. Heights under one yard should be measured to the nearest inch; from one to two yards to the nearest half-foot; when above reach height may be estimated in feet.)
c. Concealment—is nest exposed or well hidden?
d. Protection. Are thorny trees favored? Is nest placed near a wasps' hive? Can other concealing or protective devices be detected?
3. Relation of nest-site to male's singing posts

D. Nest-building
1. Activities of the sexes during nest-construction
2. Kinds of materials selected
a. How are they gathered?
b. Are they brought from near or far?
3. Time of day when building is most active
a. Number of trips per hour during sample periods
4. Number of days required to complete nest
5. Structure of nest
a. Form (cup-like, oven-shaped, pensile, etc.)
b. Dimensions, internal and external (Measurements should refer to compact body of nest, not to loosely projesting ends of straws.)
c. Weight
d. Materials of foundation, walls, lining, etc.
e. Special features for concealing contents, sheltering them from rain, or the like, if they occur

E. The eggs
1. Time of laying
a. Interval between completion of nest and laying first egg
b. Hour of day when egg is deposited
c. Interval between eggs
2. Description of eggs
a. Shape, color and texture of shell (Describe common types and extreme variations.)
b. Is the color cryptic?
c. Size (Measurements may be made with calipers at nest, to nearest half-millimeter. In presenting data, state number of eggs measured, average to 0.1 mm., and dimensions of longest, shortest, widest and narrowest eggs. Fifty eggs of each species should be measured if possible.)
d. Weight of eggs in relation to weight of bird (Its fluctuation with differences in age or weight of the layer might be studied.)
3. Size of sets
a. General (Too often only averages are stated. It is important to know the actual number of sets of each size, e.g. 5 sets of 1, 90 sets of 2, 4 sets of 3, etc. This may be abbreviated $5 \times c/1$, $90 \times c/2$, $4 \times c/3$.)
b. Analysis (The size of sets may vary with the month of laying, peculiarities of weather, first or subsequent broods, young or old layers, etc. This information is of great ecological importance.)
c. Geographical variation (If nests were found in localities differing much in latitude, altitude, rainfall, etc., the data for each locality should be given separately.)
4. Replacement of lost nests
a. How soon after eggs or nestlings were lost does the female lay again?
b. How does the replacement set compare in size with the original set?
5. Number of broods (Distinguish between replacement nests and true second broods following fledging of earlier brood.)

a. Interval between departure of young from nest and laying of next set
b. Is the same nest used for more than one brood?
c. Relation of number of broods to seasonal variations in weather
d. Relation of number of broods to latitude, altitude and other regional variations

F. Incubation
1. Role of the sexes
2. When does incubation begin (with laying of first, second, last egg, etc.)?
3. Rhythm
a. Sessions on eggs (Give extremes and average in minutes, or frequency curve.)
b. Recesses (the same)
c. Per cent of day eggs are covered (May be calculated by the formula $T = \frac{s}{s+r} \times 100$, where T = per cent of time on eggs, s = average length of observed sessions, r = average length of observed recesses.)
4. Period of incubation (If eggs are marked in order of laying, the incubation period is the interval between the laying of the last egg and the hatching of this egg. Otherwise it is the interval between the laying of the last egg and the hatching of the last egg. The period may be stated in this form: 12 days 20 hours ± 10 hours. We need to know many more incubation periods in hours.)
5. How long will the bird continue to incubate eggs that fail to hatch?

G. The nestlings
1. Feeding
a. Which parent(s) feed(s)?
b. How soon after hatching does the mother begin to feed? The father?
c. Kinds of food and how obtained
d. Mode of delivery, whether brought in bill, throat or crop
e. Rate of food-bringing for nestlings of various ages, with various numbers in nest, with changes in weather, etc.
f. Do the parents receive assistance from other birds?
2. Brooding
a. Which parent(s) brood(s)?
b. Variation of amount with age of nestlings
c. Variation with weather
3. Sanitation of the nest
a. Are the empty shells swallowed or carried away by the parents?
b. Manner of disposal of droppings
c. Removal of ants, lice, or other insect pests
4. Development of young
a. Condition at birth as to covering of down, eyes open or closed, etc. Note color of interior and corners of mouth.
b. Trace the development of the nestlings' limbs, plumage, eyesight, etc.
c. Increase in weight, as determined by daily weighings
d. Development of reactions and activities: gaping, exercising, preening, fear reactions, etc.
e. Departure from nest, whether spontaneous or induced by parents. Time of day?
5. Nestling period (Care should be taken not to cause premature departure by handling or frightening the young. The nestling period may be stated in the same manner as the incubation period, e.g. 13 days 12 hours ± 14 hours.)
a. Variation of nestling period with number in nest
b. Variation of nestling period with weather or abundance of food
c. Regional variation
6. Regulation of brood-size
a. Is there any indication that the number of eggs in the set has been adjusted, through natural selection or otherwise, to the parent's ability to nourish the young?
b. How might the brood-size be affected by the hours of daylight available to the parents for hunting food?
c. What is the relation between brood-size and the average annual mortality of the species?
7. Defense of nest and young
a. Do the parents ever attack trespassers at the nest?
b. Have the parents a diversionary display to lure trespassers from the nest?
c. Does this behavior vary with the kind of trespasser or potential enemy?
d. Does it vary with the contents of the nest, whether eggs, newly hatched nestlings or older nestlings?
8. Care of young after leaving the nest
a. Do the fledglings go into hiding or follow their parents about?
b. How long do the parents continue to feed the young?
c. At what age do they become antagonistic to the young?

H. Reproductive success
1. Causes of loss of eggs and nestlings
a. Predators of specified or undetermined kinds
b. Adverse weather
c. Desertion of nests
d. Falling of nests
e. Miscellaneous

2. Causes of failure to hatch of eggs
   a. Infertile
   b. Death of embryo
3. Causes of death of nestlings which died in nest
   a. Competition with nest-mates
   b. Insufficient food
4. Calculation of reproductive success
   a. What per cent of the nests produced at least one fledgling?
   b. What per cent of the eggs hatched?
   c. What per cent of the nestlings which hatched were fledged?
   d. What per cent of the eggs produced young that survived up to the time of fledging?
   e. What per cent of the breeding females succeeded in rearing nestlings by dint of repeated trials?
   f. Average number of young fledged per breeding pair?

X. *Development and dispersal of juveniles*
A. Feeding
1. At what age do the young begin to find food for themselves?
2. At what age do they become self-supporting?
B. Voice
1. At what age do the juveniles begin to sing?
2. Follow the development of the song
C. Plumage
1. At what age does the post-juvenal molt begin?
2. At what age does the bird acquire adult plumage?
3. Describe the sequence of plumages
D. Dispersal
1. At what age do the young leave the parental territory?
2. How far do they go before settling down?
E. Survival
What per cent of the young are lost during the post-nestling stage?
F. Reproductive maturity
1. At what age do the young birds acquire nesting territories?
2. At what age do they pair?
3. At what age do they breed?

XI. *Population and vital statistics*
A. Density of the population
1. In the non-breeding season (Give method of taking census.)
2. During breeding-season, as determined by counts of nests or singing males, and making allowance for non-breeders
B. Longevity (This can be learned only by trapping and banding.)
1. How long may the bird live under the most favorable conditions?
2. What is the life-expectancy of full-grown young birds?
3. Are full-grown young birds more likely to meet accidents than older and more experienced individuals?
4. Determine the composition of the population by age-groups
5. What are the chief causes of mortality (see VI)?
C. Sex-ratio
1. Determine if possible the ratio of the sexes at fledging
2. Determine the sex-ratio of adults.

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A SELECTED BIBLIOGRAPHY OF ECOLOGICAL LIFE HISTORY MATERIAL ON NORTH AMERICAN BIRDS

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APPARATUS FOR IMITATING CHANGES IN SALINITY OF WATER OCCURRING IN NATURE DURING A COMPLETE TIDAL CYCLE

The apparatus is designed to simulate the changes in salinity taking place in inter-tidal basins which have a considerable inflow of fresh water during low water stages. The design incorporates the ideas of the several staff members of the Milford Laboratory. The chief task of the apparatus is to reduce gradually within a 6-hour period, as if during ebb tide, the salinity of the water to that of almost fresh water and then, during the following six hours, as on the flood, gradually increase it to the full salinity usually prevailing during the high water stages.

Although the apparatus was made primarily for studies of the effects of changing salinity upon the behavior of oysters, it is equally suitable for experiments of the same nature on other invertebrates and also fishes. The details of the apparatus are shown in figure 1.

Gradual changes in salinity are accomplished by the continuous changing proportions of sea and fresh water passing through the mixing unit, *A*. It is achieved as follows: A supply of fresh water is taken from the constant level vessel, *F*, and that of salt water from a similar vessel, *S*. Both vessels, of course, are provided with overflows, *O*. The water from the constant level vessels flows through the tubes, *f* and *s*, to the mixing unit, *A*. This unit, enlargement of which is shown in the right half of figure 1, consists of a block, *B*, with two square orifices, f_1 and s_1, for the passage of fresh and salt water respectively. The relative position of these orifices is such that when one of them, s_1, fully coincides with the square opening leading into the tube, s_2, of the block, *C*, undiluted sea water only is flowing through to the unit. However, when the block, *B*, is slowly moved down by the gear, *D*, the area of contact between s_1 and s_2 diminishes, while part of the square, f_1, comes against the square opening leading into the tube, f_2, thus allowing some fresh water to flow through. As the downward movement continues, the area of contact of f_1 and f_2 increases, while that of the orifices, s_1 and s_2, decreases, correspondingly increasing the quantity of fresh water passing through the mixing unit, *A*, and decreasing that of the salt water. Eventually, six hours later, at the end of the period corresponding to the end of ebb tide, only fresh water will be flowing through the mixing unit, *A*, while the salt water will be cut off.

During the next six hours the process will be reversed by the opposite movement of the gear, *D*, decreasing the flow of fresh and increasing that of salt water, until again six hours later, corresponding to the time of the end of flood tide, only salt water will flow through the unit, *A*.

The up and down movement of the block, *B*, containing orifices f_1 and s_1 is exercised by the gear, *D*. The movement of the gear itself is caused by the change of the position of the float, *E*, which is attached to the rod, *G*, by a string going over a pulley. This float rises or falls with the water level of the tank, *I*. When that level is at its highest, *H*, corresponding to the high water stage in nature, only salt water will flow through the mixing unit, *A*, while at the lowest point, *L*, fresh water only will flow.

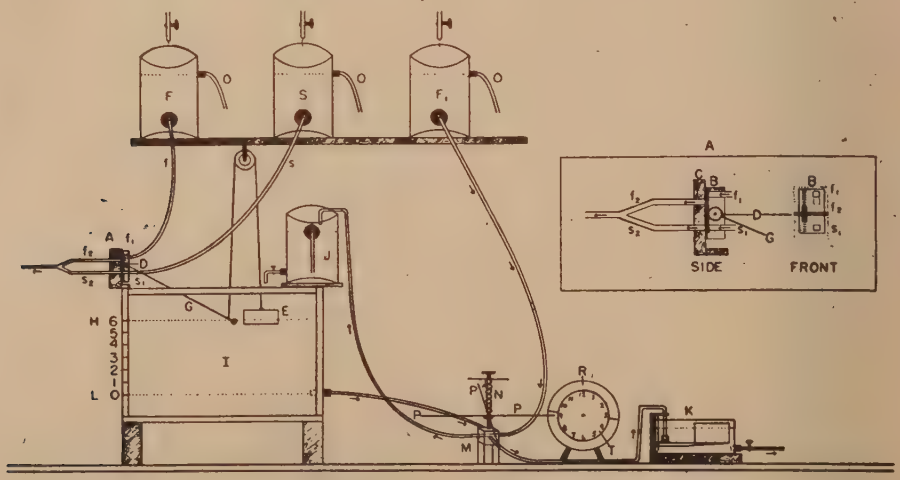

FIG. 1. Description in text.

Since in our waters the average period between the high and low water stages is approximately six hours, the change of the water level in the tank, *I*, from *H* to *L* and vice versa is also made in six hours.

The rising of the water level and, therefore, of the float, *E*, is accomplished by filling the tank, *I*, with water running at a constant rate from the constant level jar, *J*. This flow is so regulated that it fills every hour exactly one-sixth of the distance between levels *L* and *H* of the tank, *I*. The emptying of the vessel, *I*, and lowering of the float, *E*, is done by draining the water at the same constant rate at which it was filled. The water is emptied through the constant level chamber, *K*, description of which has already been given (Loosanoff and Engle, '47).

Since the processes of filling and emptying the tank, *I*, alternate every six hours, a device is needed to initiate the change from one to the other. During the filling the water from the constant level, F_1, runs, as indicated by the arrows in figure 1, through a hard rubber, four-way stopcock, *M*, to the vessel, *J*, and then flows at a constant rate into the tank, *I*. After six hours the stopcock is given a quarter turn. This cuts the flow of the water in the tank, *I*, and simultaneously starts its emptying through the same stopcock and chamber, *K*. After another six hours the cock is again given a quarter turn which reverses the process.

The turning of the four-way stopcock, *M*, is done by the tightly wound, coiled spring, *N*, attached to the head of the cock. The turn is made every six hours when one of the four rods, *P*, passes through the slit of the disc, *R*, attached to the hourly hand of the clock, *T*. The slit is so designed that only one rod goes through while the rod following it is stopped by the face of the disc. Thus, the time unit works automatically and precisely, turning the stopcock once every six hours.

The entire apparatus is versatile in the respect that the points of higher or lower salinities can be regulated according to the need of the experimenter. For example, if instead of fresh water the lowest salinity needed for the experiment is 10.0 parts per thousand, then by placing over *F* two more constant level vessels, one for salt and the other for fresh water, and by regulating the flow from these vessels into *F* a mixture of the desired salinity can be easily obtained.

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APPARATUS FOR MAINTAINING SEVERAL STREAMS OF WATER OF DIFFERENT CONSTANT SALINITIES

The apparatus was designed for experiments in which it is necessary to keep simultaneously several groups of animals in running water of different but constant salinities. It has successfully been used in our laboratory during the last three years for observations of various aspects of the behavior of oysters, different species of clams, mussels, sponges and other invertebrates. It is equally suitable for experiments with fishes. The apparatus is simple and can be readily assembled and installed in any laboratory where supplies of sea and fresh water are available.

The apparatus consists of two jars, *F* and *S*, serving as reservoirs for fresh and salt water respectively (Fig. 1). The jars are filled through intakes, *I*, at such a rate that the excess water is continuously escaping through the overflows, *O*. Thus, the water level in each jar is constant. From the opening near the bottom of each jar a main tube leads to several branch tubes. These branch tubes are so paired that in each unit a fresh water tube (solid lines, Fig. 1) is placed next to the salt water tube (dotted lines, Fig. 1). Each tube has in its middle section a regular stopcock (*C* or C_1). By manipulating a pair of the stopcocks any desired mixture of sea and fresh water may be obtained. Above the cocks the flow of fresh and salt water is united by the glass *Y* and then passes into the chamber, *M*, where it is thoroughly mixed before flowing through the tube, *L*, leading to the tray or aquarium. By turning off one of the cocks the unit may be converted to supply either fresh or undiluted sea water.

The number of mixing units is determined by the requirements of the experiments. In our laboratory we often conduct experiments calling simultaneously for running water of salinities of 3.0, 5.0, 7.5, 10.0, 12.5, 15.0 and 20.0 parts per thousand.

Experience has shown that if the branch tubes are placed in a horizontal position, air bubbles will often form in them fully or partly blocking the orifices of the stopcocks, thus

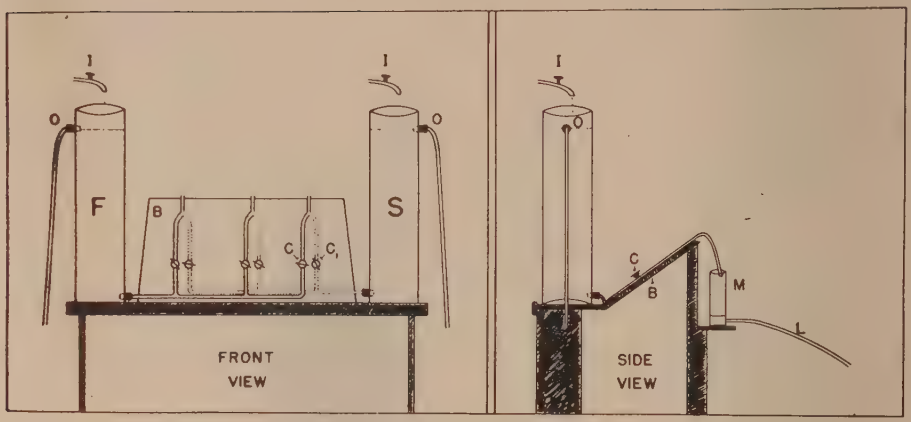

FIG. 1. Description in text.

changing the rate of flow of the fresh or salt water, or both. This commonly happens in winter when the temperature of the water is considerably lower than that of the air of the room. To avoid this difficulty the entire system of tubes is mounted on a board elevated at approximately a 45° angle (Fig. 1, side view). As soon as an air bubble begins to form, it passes through the orifice because of its tendency to rise and is carried away by the current.

The important feature of the apparatus is that it provides a continuous flow through the vessels containing the experimental animals. This is a distinct advantage over the old but, nevertheless, still widely used method where the animals are kept in still water, because the continuous exchange assures a rapid elimination of the waste products forming in the vessels. Furthermore, the constant current caused by the flowing water is another desirable factor which helps to maintain a more natural condition during the experiment.

Because fresh water is often deficient in food it may be necessary to enrich the mixtures of low salinities with food organisms. This is accomplished by installing a large container with a rich plankton culture which would continuously drip into the jar, *F*, and from there would be distributed together with fresh water to the mixing chambers, *M*, from which it would be carried to the trays with the experimental animals.

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EXPERIMENTAL DETERMINATION OF THE AUTOSELECTED TEMPERATURE IN THE CHICKEN LOUSE, *CUCLUTOGASTER HETEROGRAPHUS* (NITZSCH) [1]

INTRODUCTION

Animals exhibit various relationships to temperature conditions in their environments. Each physiological process proceeds within a certain, often narrow, range of temperature conditions and usually exhibits some maximum of efficiency at a particular optimum temperature. These temperature limits and optima are reflected in the bionomics of an organism, determining the range of conditions under which it can survive and its degree of success in reproducing and maintaining populations in particular environments. Frequently animals are so adjusted to temperature conditions that they will select from a range of available temperatures one which is essentially optimum for the individual or the species (Heilbrunn, '43).

The experiments reported here were conducted with insects which are normally ectoparasitic on homoiothermic animals and which, therefore, are ordinarily found in an environment of relatively constant temperature. An attempt was made to learn whether these insects would automatically select any definite tempera-

[1] This material is from a thesis submitted to the Faculty of Indiana University in partial fulfillment of the requirements for the degree of Master of Arts. Contribution No. 373 from the Department of Zoology, Indiana University.

ture or range of temperature and if such an autoselected temperature would approximate the conditions of their usual habitat.

I am indebted to LaMont C. Cole for valuable suggestions and criticisms during the course of this investigation.

Materials and Methods

A mallophagan of the suborder Ischnocera, *Cuclutogaster heterographus* (Nitzsch) (Family Philopteridae), which occurs exclusively among the feathers of the head and neck of the chicken, was selected. This species was chosen for particular study because of the ease with which adequate numbers may be reared in the laboratory and because it has been studied relatively well from the standpoint of culture methods and life cycle.

It is known that many insects will tend to congregate when they are exposed to a range of temperature conditions (Fraenkel and Gunn, '40). The temperature at which aggregation occurs, sometimes called the "preferred" temperature, is best termed the autoselected temperature and is usually determined experimentally in either of two principal types of apparatus. One type of apparatus (Martini, '18) is a long metal gradient, heated at one end and cooled at the other. Various modifications of this apparatus have been constructed for use with a variety of animals (see Fraenkel and Gunn, '40). Several objections have been raised concerning its use. The temperature may become stratified in such an apparatus, thus making observations on flying insects rather difficult. Furthermore, the metal and the air may be at different temperatures, and larger insects may not have sufficient latitude for wanderings within a temperature zone. The second type of apparatus consists of a source of heat located in the center of a disc with the temperature gradations in concentric rings moving out from the heat source. The proponents of this type of apparatus claim that it gives adequate room for wandering. However, it is extremely difficult to heat the disc evenly, and it is even more difficult to plot accurate temperature zones. With the long gradient apparatus, observations are taken at definite time intervals and the positions of aggregations of animals noted. With the disc type apparatus, the observer usually traces the path of the insect and considers the area with the greatest number of tracings as the "preferred." This procedure may be criticized on the basis that random wanderings take them to one place, and aggregations tend to keep them there, and that animals frequently tend to show reduced locomotion near the area of their autoselected temperature. The insects must also be kept moving in order to give a tracing, which may be a very unnatural condition. It is not the actual track of the insect that is important but rather how it selected the point and how long it remains.

Results of others seem to show that temperature preferences are for zones rather than exact points, although it is convenient to express the preference as a point. It is best that the point represent aggregations of fifty to eighty per cent of the animals rather than the entire one hundred per cent since a few scattered observations lying at the end of the gradient, where the curve tails off, will be unduly weighted. The arithmetic mean gives little indication of the extent of the preferred range unless some measure of sampling variability such as the standard error is also employed.

Homp ('38) determined the "preferred" temperature range of the human louse (*Pediculus*) by recording tracks in a linear gradient. Her records showed a decidedly "convoluted" path in the area around 30° C., indicating to her a preferred zone. Wigglesworth ('41) placed lice in a linear gradient and noted only the areas of clustering. His results agree well with Homp's, with the greatest congregation occurring at 28° C. to 31° C. The response of the lice was to air temperature and apparently not to radiant heat.

Experiments and Results

A small colony of adult chickens was kept in rather crowded, dark quarters to encourage louse development in order to insure an adequate supply of Mallophaga for experiments. Their feed was supplemented to insure an abundance of the necessary nutrients. Extreme cold was avoided as was also extreme heat since both seemed to inhibit louse production. Ten birds furnished enough lice for the experiments to be reported.

The gradient apparatus used (fig. 1) is a modification of one described by Wigglesworth ('41) for Anoplura. It consists of a long chamber secured within a larger chamber filled with sand, and the whole heated to different degrees along its length by means of light bulbs. Temperature control was achieved by varying the size of the light bulbs and their distance from the apparatus. Thermometers placed at regular intervals in the sand recorded the temperature transferred to the inner gradient. This recorded temperature was carefully checked with a thermocouple placed on the actual walking stratum of the apparatus and a correction figure calculated after the thermocouple readings were plotted against the thermometer readings. This provides a simple yet extremely accurate way of recording the temperature since, with the correction known, the thermometer becomes an excellent indicator of the variations in temperature.

The following procedure was used to deter-

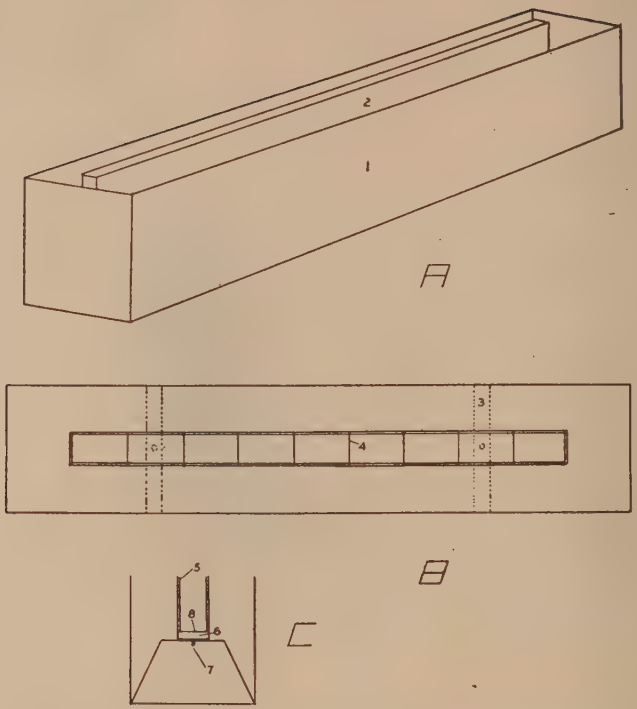

FIG. 1. Temperature gradient apparatus for determination of autoselected temperatures in small insects. *A*. View of apparatus: (1) metal box containing moist sand and mounted over heat source; (2) gradient channel measuring ¾ inch wide × 2 inches deep × 16 inches long placed within box of sand. *B*. Top view of apparatus; (3) support for gradient channel; (4) ⅜ inch partition at bottom of gradient channel to allow solutions of different kinds to be placed under the gradient. *C*. Section of apparatus: (5) bottomless shell inside gradient channel to hold down different substrata; (6) space to be filled with water or other solution to control humidity; (7) pin on bottom of gradient channel to secure it to support (3); (8) substratum of fine mesh screen wire resting on partitions (4), overlain by walking stratum, the whole held in place by the inner lining (5).

mine the temperature preference of *C. heterographus*. Ten adult lice were removed from a fowl and placed in the chamber of the apparatus. Lice might be introduced at any point since it was found to have no effect on the temperature at which aggregation ultimately occurred. The time was noted and the positions of the lice were marked on a chart. At five minute intervals their positions were noted until one-half hour had elapsed, at which time they were removed. The humidity was unregulated and all runs were made in the dark because preliminary trials showed that the presence of daylight distorted the aggregations in such a manner as to suggest a negative reaction to light. Preliminary runs were made in a gradient extending from 25° C. to 65° C. in order to determine the general region in which the lice congregated. The aggregations were found to occur constantly between 35° C. and 55° C. and in future experiments, therefore, the gradient was adjusted to extend between these limits. After one-half hour in the gradient, the lice were always congregated in a small area. When placed in the gradient at different positions it was noted that those placed in the colder end were much slower to reach the area of aggregation than those placed at the hot end. This would be expected, however, from the common observation that activity in poikilotherms tends to vary directly

TABLE I. *Autoselected temperatures for* 50° C. heterographus

Temp. °C.	No. of lice
33.4	1
38.4	2
39.4	1
40.4	2
41.3	10
42.3	15
43.3	10
44.3	5
46.3	1
47.3	1
48.3	1
49.3	1

with the temperature. Fifty lice were run through the gradient in samples of ten each. Table I shows the analysis of the grouping of the entire sample.

The extreme range of temperature over which the lice were distributed in the gradient extended from 33.4° C. to 49.3° C. with a mean value of 42.49 ± 0.34° C. The standard deviation of the distribution of fifty autoselected temperatures was 2.43° C., indicating that the observed mean value probably lies very close to the actual "preferred" temperature for these insects under the conditions of the experiment.

Discussion

It may be seen from a study of the results obtained that the selected temperature for Mallophaga as typified by *C. heterographus* is distinctly above that of other insects. It is possible that one source of this disagreement is a result of the different techniques and conditions used by the various experimenters. Another and possibly more plausible explanation, however, lies in the habits of the Mallophaga, which normally never leave their host. The eggs are laid and hatch among the downy feathers close to the skin. Observations made on several fowls at different times with the thermocouple showed the average skin temperature to be 41.5° C. The optimum selected temperature of 42.49 ± 2.43° C. thus agrees very favorably with the temperature of the normal habitat of the lice. It is suggested, therefore, that the habits of this insect explain its rather high "preferred" temperature.

Wilson ('34) succeeded in keeping lice alive in the incubator in excess of thirty-six days by using a temperature of 33° C. to 34° C. Barber ('21) kept the insects alive twenty-four days at 35° C. while Ansari ('44) succeded in keeping one specimen alive for eighty-five days at 39° C. On the basis of the work here reported it is suggested that the optimum culture temperature should be around 42° C., assuming that all stages in the life cycle respond as the adults do. There is no apparent reason for employing temperatures below that of the normal habitat.

Homp ('38) and Wigglesworth ('41) found the "preferred" temperature for the Anoplura to be in the neighborhood of 30° C. At first comparison, this great difference in temperature selection between two ectoparasites of homoiothermic animals appears irreconcilable. However, the fact that the body louse spends much of its time in the clothing of the host and even lays its eggs there suggests an explanation for the difference.

The Anoplura might be expected to exhibit a wider latitude than the Mallophaga with a rather low "preferred" temperature resulting from their habit of leaving the host to breed, and a high thermal death point enabling them to feed on the host.

Summary

1. At unregulated humidity and in the absence of light, the "preferred" temperature of *Cuclutogaster heterographus* (Nitzsch) was found to be 42.49° C. ± 0.34° C.

2. The average skin temperature of the head and neck (the location in which this mallophagan is usually found) of the domestic fowl was found to be 41.5° C.

3. It is suggested that the optimum culture temperature is in the vicinity of 42° C.

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THE FRESHWATER MEDUSA, *CRASPEDACUSTA SOWERBII*, IN MATOAKA LAKE, WILLIAMSBURG, VIRGINIA

The freshwater jellyfish, *Craspedacusta sowerbii* Lankester, has been described from at least 19 of the 48 states (Schmitt, '39). In spite of an apparently widespread distribution it is sufficiently rare that records of its occurrence are noteworthy.

Approximately 200 medusae of this species were seen in Matoaka Lake, Williamsburg, Va., on July 18, 1949. On August 1, 1949, the lake was revisited. About 25 individuals were observed in a different part of the lake.

Matoaka Lake is a small, artificial body of water about 57 acres in area. Its maximum depth is about 21 feet. The medusae were found near the surface in the open part of the lake where the water was deep.

There is no previous record of the occurrence of *Craspedacusta sowerbii* in Matoaka Lake. The freshwater jellyfish has, however, been reported in other parts of Virginia. Schmitt ('39) reported that specimens of the medusa were collected in several quarries around Richmond in 1933, 1935, 1936, and 1937. Other specimens were found in a goldfish pond in Alexandria, Virginia, in 1933. Hamaker and Milne ('37) reported *Craspedacusta* from Crystal Lake, near Lynchburg, Virginia.

Specimens from Matoaka Lake were sent to the United States National Museum and were identified by Dr. Ralph W. Dexter of Kent State University.

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PARIS ECOLOGY COLLOQUIUM

As one of a series of international colloquia, the Centre National de la Recherche Scientifique, with the cooperation of the Rockefeller Foundation, sponsored a colloquium titled "Ecologie des Groupements Animaux et Mixtes" in Paris from February 20 to 25, 1950. Professors Prenant and Pacaud of the Sorbonne made most of the arrangements. Two half-day sessions were held each day. Ten such sessions met at the Curie Institute, one at the Trappes Meteorological Station, and the final session in the Cauchy Amphitheater of the Sorbonne. The size of the audience ranged from 40 to 70 persons.

Only two or three papers were presented at each half-day session, and as a consequence there was ample time for discussion, which often proved lively and stimulating. Contributions covered a wide variety of terrestrial, marine, and fresh-water phases of animal ecology and general ecology; the majority were of a summarizing or synthesis nature, but a few dealt with narrow and specific phases of ecology. Most of the papers were delivered in French or English, but a few were given in German. An able interpreter implemented the discussion following each paper.

The tenor of the Colloquium and the many informal conferences were truly international and cooperative. Sixteen papers were given by representatives from France, four from England, three from Austria, two from Denmark, and one each from Sweden, Switzerland, Belgium, and the United States. All of the contributions and associated discussions are scheduled for publication in a single volume.

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EDWIN BOOTH POWERS, 1880–1949

Dr. Edwin Booth Powers, a former president of the Ecological Society, died very suddenly at his home on August 25, 1949. He had been in good health until the moment of his death, caused by coronary thrombosis.

He was born on August 6, 1880, in Ellis County, Texas, the son of William Wilson and Evaline Woods Powers. In 1918 he married Pauline Watkins; they had two children, William W. Powers, now of Philadelphia, and Edwine, now Mrs. Williston Cox of Louisville, Tennessee. His widow and children survive him.

He graduated from Trinity College, Texas,

in 1906. In 1913 he received the Master of Science degree from the University of Chicago and in 1918 the Doctor of Philosophy degree from the University of Illinois. In between the times engaged in graduate study, he taught in high schools and later in his alma mater, Trinity College. After receiving his doctor's degree, he taught successively at Colorado College, the University of Nebraska, and The University of Tennessee. In 1925 he was appointed head of the Department of Zoology at The University of Tennessee, a position he held until 1947 when he retired from teaching and administrative work to full-time research. Several of his summers were passed at the Puget Sound Biological Station, the Franz Theodore Stone Laboratory, and similar institutions.

In 1948 he prepared a list of his publications which serves well to illustrate where lay his research interests. The list numbers sixty-one titles; by far the majority deal with these topics: oxygen and carbon dioxide tensions in both fresh and salt water, the respiration of fishes, migration of salmon, and causes of fish mortality. The largest number of titles concern the respiration of fishes. The tenacity of his research interest is indicated by the fact that he published papers in each of the four topics mentioned above throughout the approximately twenty years of his active publication. His interests, however, were not limited to these topics; one published note is on the behavior of a mammal, another on birds.

At The University of Tennessee he taught courses in physiology and in field zoology, the latter being primarily a course in animal ecology. Further evidences of his interest in ecology are his memberships in the Ecological Society of America and in the Limnological Society of America, as well as in several other scientific societies. He was president of the Ecological Society of America for the year 1933–34, Associate Editor of Ecology from 1925 to 1930, and Associate Editor of *Ecological Monographs* from 1935 to 1939.

An outstanding characteristic of Dr. Powers was his diligence and capacity for hard work. He was at his desk working on a manuscript when he died.

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PRECIPITATION IN RELATION TO ALTITUDE IN CENTRAL UTAH

Occupance of arid lowlands of the western United States is greatly influenced by relatively abundant precipitation in the mountains. This precipitation supports forests and forage, important in the lowland economy, which cannot grow at low elevations. Most important of all, mountain precipitation is the chief source of water for agricultural, industrial, and domestic use; and civilization in most of the West would be impossible without it. Mountain precipitation has a sinister aspect, too, in that it may give rise to destructive floods following misuse and depletion of vegetal cover (Bailey, Craddock, and Croft '48).

Vegetal Zones

The Wasatch Plateau, which reaches a maximum elevation of 11,282 feet, has a pronounced north and south trend. On the east it is flanked by Castle Valley and drains into the Colorado. On the west it is flanked by Sevier and Sanpete Valleys and drains into the Great Basin. Elevations of these valleys lie mostly between 5,000 and 6,000 feet. Ephraim Canyon, at latitude 39°20′, drains part of the west front of the Plateau. For about 1 mile east of the town of Ephraim (elevation 5,543 feet), the rise is gradual. As the Plateau front is approached the rise becomes steeper, and in about seven airline miles an elevation of 10,200 feet is reached at the head of Ephraim Canyon.

Broad vegetal zones succeed each other as elevation increases. Their limits are not precise; the zones tend to interfinger because of variations in exposure and soil parent material. Dominant native vegetation of the valley zone is sagebrush, up to an elevation of about 6,000 feet. A juniper-pinyon (*Juniperus utahensis, Pinus edulis*), woodland zone may be distinguished particularly on warm, rocky sites, from the beginning of the foothills up to about 6,500 feet.

A mountain brush zone extends to an elevation of about 7,800 feet. On southerly exposures the dominant species is oakbrush (*Quercus gambellii*), although manzanita (*Arctostaphylos patula*) is locally dominant on sandstone outcrops, and mountain-mahoganies (*Cercocarpus montanus* and *C. ledifolius*) on thin-soiled, rocky sites. On northerly exposures in this zone maplebrush (*Acer glabrum*) shares dominance with oakbrush or completely replaces it. The oakbrush and maplebrush communities are successionally transitional to conifers—pinyon and juniper (often *J. scopulorum*) in the lower part of the zone, and white fir (*Abies concolor*) in the upper part.

An aspen-fir zone is found between elevations of about 7,800 and 9,500 feet. Here aspen (*Populus tremuloides*) is dominant, especially on gentle terrain. Aspen is giving way successionally to fir and spruce—*Abies concolor*

and *Picea glauca* in the lower part of the zone, *A. lasiocarpa* and *P. engelmanni* in the upper part. These successional trends toward conifers, as in the mountain brush zone, reflect protection from fire during the last half-century.

A subalpine zone begins at about 9,500 feet. Subalpine vegetation on northerly exposures consists of spruce-fir forests (*P. engelmanni* and *A. lasiocarpa*) and, on southerly exposures and level areas, mainly of parkland in which patches of spruce and fir may occur in extensive areas dominated by grasses and herbs. The Wasatch Plateau does not rise sufficiently high to develop a well-marked timberline or a tundra-like alpine zone.

The limits of these broad vegetal zones appear to be set by conditions of water stress. Precipitation increases and temperature decreases with elevation, giving a transition from near-xeric to progressively more mesic habitats between the valley and the aspen-fir zone. This trend continues into the conifer forests on northerly exposures of the subalpine zone, but on warmer sites that are more exposed to wind a less mesophytic, herbaceous vegetation results. The conclusion is evident, from this thumbnail sketch of vegetation and habitats, that an understanding of the variation of precipitation with altitude is important to an understanding of the plant communities.

Because few precipitation records are available from mountains as compared with inhabited lowlands, and because of the practical importance of mountain precipitation in resource management, its characteristics need to be better understood. The present paper is a contribution in this direction. On the basis of records from Ephraim Canyon, on the west front of the Wasatch Plateau in central Utah, the specific purposes of this report are to summarize the relation between altitude and amount of precipitation, variations in this relation due to season and topography, and 15 years' data in addition to those already published (Costello and Price '39, Price and Evans '37) as characterizing precipitation of this area.

Character of Records

The four stations at which observations were made are in the following vegetal zones: Ephraim in the valley sagebrush zone, Oaks in the mountain brush zone, Headquarters in the aspen-fir zone, and Meadows in the subalpine zone.

The data reported here cover the 15 years, 1934 to 1948 inclusive. Precipitation at Ephraim was measured in a standard can or weighing intensity gage. At other stations, summer precipitation was measured either in standard cans or intensity gages, winter precipitation in Marvin or Alter storage gages.

A complete 15 years' record by months exists for the lower three stations. In the subalpine zone the Meadows record is incomplete. First records in the subalpine zone were taken at Alpine, elevation 10,100 feet, just below the crest of the Plateau at the head of Ephraim Canyon. Between 1934 and 1941 intermittent records were also taken at Meadows, 0.4 mile from Alpine and 240 feet lower. Precipitation catch at Meadows during this period was often greater than at Alpine. As snow survey and observational evidence do not indicate that the Meadows catch is increased by drifting, the difference must be attributed to greater wind velocities at Alpine which would deflect rain and snow from the gage orifice. The Alpine station, therefore, was discontinued and a continuous record started at Meadows in 1942.

Meadows precipitation divided by Headquarters precipitation for this unbroken period of record gives a factor of 1.090. Gaps in the Meadows record for 64 months, 1934 to 1941, have been filled by applying this factor to corresponding monthly totals from Headquarters. A test of the validity of this factor was made by predicting values for months of record at Meadows during 1934 to 1941. Comparing predicted and actual values by the t-test with $n = 32$, differences were found to be non-significant. It therefore appears that the equation

$$P_M = 1.090\ P_H$$

is reasonably valid and that substitution of the missing data for Meadows is justified.

Annual Precipitation

Precipitation for the period 1934 to 1948 was slightly above average in central Utah. Nine of the 15 years at Manti (elevation 5,575 feet), 7 miles south of Ephraim, were above the long-time average based upon records extending from 1894. As compared with an annual average of 12.26 inches from 1894 to the present, the average for 1934 to 1948 was 13.00 inches. Average annual precipitation at Oaks climatic station in the oakbrush zone was 20.10 inches, 1934 to 1948, as compared with 17.51 inches, 1914 to 1934. At Headquarters in the aspen-fir zone it was 29.53 inches, 1934 to 1948, as compared with 29.48 inches, 1914 to 1934.

As shown in table I, average annual precipitation from 1934 to 1948 varied from 10.88 inches at Ephraim to 32.21 inches at Meadows. Difference in elevation is 4,317 feet.

Variation, as expressed by standard error of the mean, tends to increase as elevation and average amount of precipitation increase. The last column in table I shows, however, that amount of precipitation increases more rapidly than variation, since the coefficient of variation —standard deviation in relation to the mean—

TABLE I. *Annual precipitation, 1934 to 1948 inclusive, at various elevations in Ephraim Canyon, and variation*

Station	Elevation	Annual precipitation	Standard error	Coefficient of variation
	feet	inches	inches	pct.
Ephraim	5,543	10.88	0.76	27.0
Oaks	7,655	20.10	1.08	20.8
Headquarters	8,850	29.53	1.48	19.4
Meadows	9,860	32.21	1.42	17.0

decreases with altitude. Thus, although absolute variation is greater at higher elevations, relative variation is less. A similar relation is often found in comparing variation in precipitation of arid and humid regions.

Relation to elevation.—Figure 1 shows that the relation between annual precipitation and elevation in Ephraim Canyon is essentially linear. Using average values for the four stations listed in table I, precipitation increases at the rate of 5.17 inches per thousand feet rise in elevation (broken line).

The departure of the Headquarters value from this line is comparatively large and is positive. These facts suggest that a "canyon effect" (Baker '44, Hall '41), increasing precipitation at this station, is produced by nearness of a high steep cliff facing northwest, which undoubtedly influences the prevailingly westerly and southwesterly winds. If the Headquarters average is therefore excluded, the line adjusted to the other three points gives a better fit. It now shows precipitation to increase 4.94 inches per thousand feet rise in elevation. The relation is expressed by the equation

$$P = 0.00494\,E - 16.95$$

where precipitation (P) is expressed in inches and elevation (E) in feet.

Further justification for eliminating Headquarters from this regression is given by 28 months of precipitation records at Snowberry. Snowberry lies about a mile away from Headquarters and the cliff that is believed to have a pronounced effect upon wind currents there. It is 400 feet lower than Headquarters. Snowberry values were first corrected to Headquarters elevation by regressions of precipitation on elevation by selected periods. (These regressions are given in table II.) The corrected values are lower than Headquarters values, and consistency in the differences is demonstrated by a highly significant t-test. As will be seen

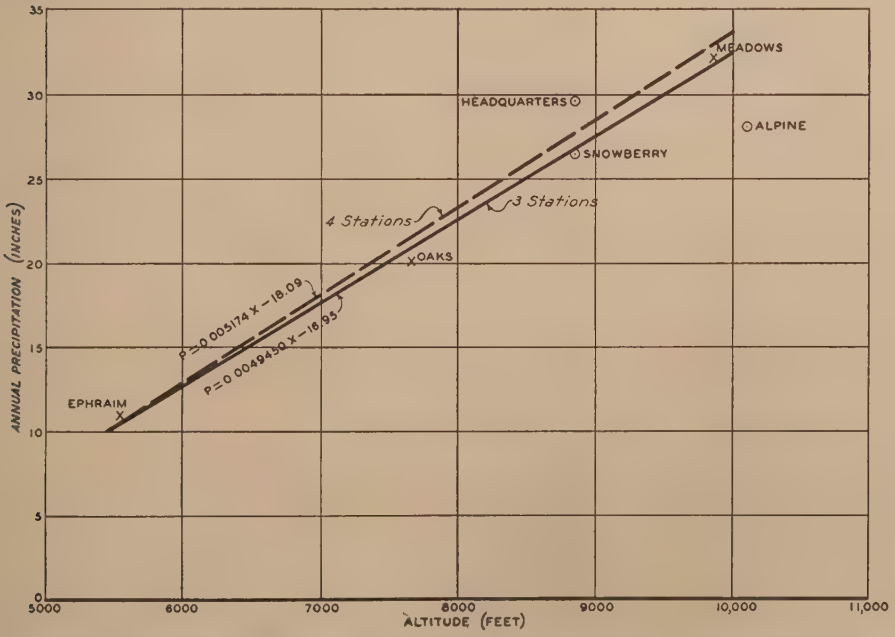

FIG. 1. Annual precipitation in relation to altitude on basis of records at Ephraim, Oaks, Headquarters, and Meadows is shown by broken line. Relation with Headquarters eliminated is shown by solid line.

TABLE II. *Mean monthly precipitation by selected periods*

Station	Elevation	Periods				
		Feb.-April	May-June	July-Sept.	Oct.-Jan.	Annual (av.)
	Ft.	*In.*	*In.*	*In.*	*In.*	*In.*
Ephraim	5,543	1.11	0.94	0.72	0.88	0.91
Oaks	7,655	2.32	1.58	1.04	1.72	1.68
Headquarters	8,850	3.77	1.92	1.44	2.51	2.46
Meadows	9,860	3.95	2.19	1.56	2.80	2.68
Monthly increase with elevation, inches per thousand feet[1]		0.66	0.29	0.19	0.45	0.41

[1] Regressions derived from Ephraim, Oaks, and Meadows; Headquarters excluded.

from figure 1, the corrected Snowberry average lies close to the solid trend line of the three principal stations.

Zone of maximum precipitation.—In studying Ephraim Canyon records between 1914 and 1934, Price and Evans ('37) reported 29.48 inches at Headquarters and 28.01 inches at Alpine ("spruce-fir zone"), a decrease of 1.2 inches per thousand feet. With this conclusion the increase of 4.94 inches per thousand feet, described in the present paper, over essentially the same elevational range, is in strong contrast.

Price and Evans' data were subject to two kinds of error. First, the Alpine gage, situated on a wind-swept slope, was probably prevented by wind turbulence from catching a full sample of precipitation (Hayes '44), an error to which the Meadows record is less liable. To illustrate difference in windiness, the mean velocity observed at Meadows during a 36-day period in 1948 was 4.2 miles per hour, whereas at Alpine during the same period it was 6.1. This was a fairly quiet period. During storms the difference is probably much greater. The second kind of error was the canyon effect from the cliff above Headquarters, already mentioned, that tends to augment the catch there. These two kinds of error, making catch at the higher elevation abnormally low and catch at the lower elevation abnormally high, gave an apparent decrease in precipitation with altitude between Headquarters and Alpine. It also resulted in an apparent zone of maximum precipitation in the aspen-fir zone. The data presented here show the relation between precipitation and altitude to be essentially linear between 5,543 and 9,860 feet, annual precipitation increasing steadily at the rate of 4.94 inches per thousand feet. They also indicate that within this elevational range no zone of maximum precipitation exists.

Data published by Hart ('37) for the southern Rocky Mountain region also indicate a linear relation between precipitation and altitude. They give no evidence of a zone of maximum precipitation up to an altitude of at least 11,660 feet. Other investigators, notably Lee ('41), working in the Sierra Nevada, report a zone of maximum precipitation between 4,000 and 8,000 feet elevation. Kittredge ('48) suggests that deficient gage catch of snow driven by strong winds at high elevations in the Sierra may be responsible for the apparent decrease of precipitation with increasing altitude, pointing out that "the water equivalent of the snow on the ground on Apr. 1 recorded in the snow surveys at the altitudes above 8,000 feet is greater than the figures purporting to give the total annual precipitation at those elevations." Although a zone of maximum precipitation may exist under some climatic and topographic conditions, it clearly does not under all.

SEASONAL PATTERN

Monthly increments of precipitation show a pronounced seasonal pattern (fig. 2). During February, March, and April monthly increment is greater than average; during May and June it is slightly less than average; during July, August, and September it is markedly less than average; and during October, November, December, and January it is approximately average. Thus there appear to be two well-marked seasons, late winter (February, March, and April) with precipitation above average, and late summer (July, August, and September) with precipitation below average. The other periods are more or less transitional in character between these seasonal crests and troughs (table II).

An analysis of variance, years versus periods, gave a highly significant difference between periods for all stations but Ephraim. This indicates considerable consistency from year to year in the periods selected and hence suggests that the pattern is a real one and is not accidental.

Relation to altitude.—Rate of increase of precipitation with altitude varies rather markedly between periods as shown at the bottom of table II. It is at a maximum in the wet winter period, February to April, and at a minimum

in the dry summer period, July to September. This differential, and indeed the seasonal pattern itself, are doubtless related to the fact that precipitation is received from different sources in winter and in summer, but just how they are related is not clear.

The sources of precipitation for the four states, Utah, Colorado, Arizona, and New Mexico, have been outlined by Dorroh ('46). During winter months the main source is Polar Pacific air invading from north, northwest, or west. Convergent type storms produced by these invasions are general in extent. Forced to pass over the Wasatch Plateau, these air masses are subjected to orographic influence to a degree reflected in the pronounced precipitation-altitude relationship of winter months.

The main source of summer precipitation, on

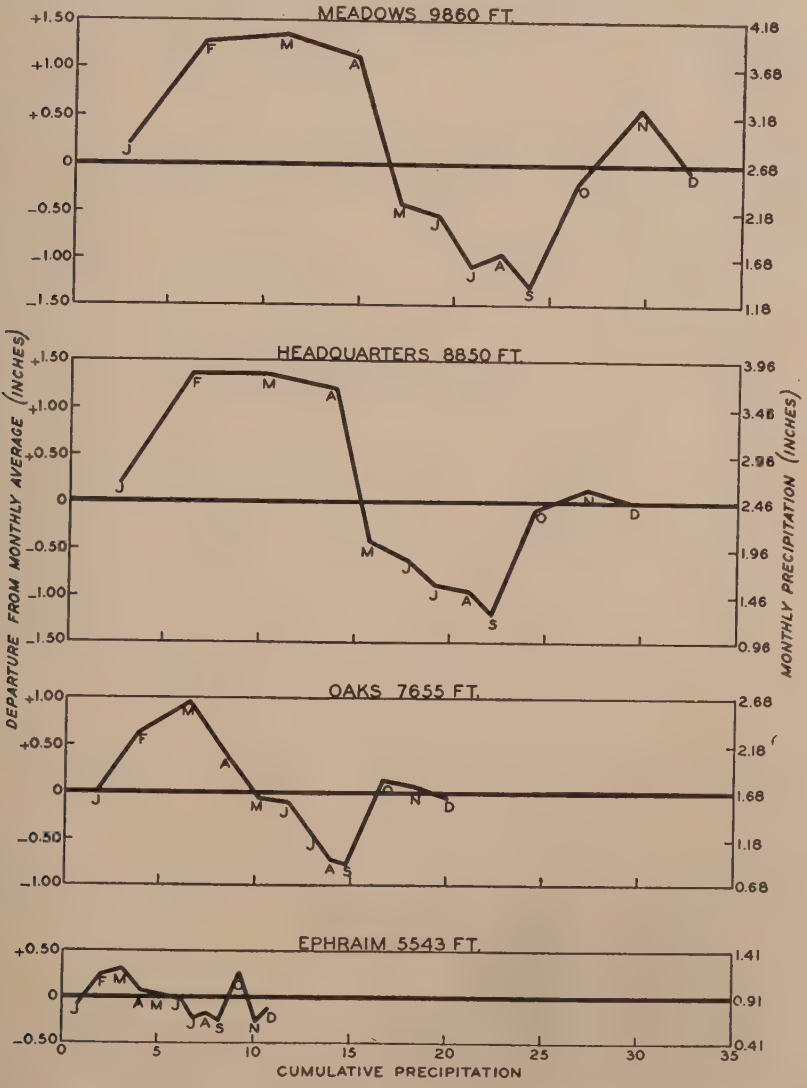

FIG. 2. Cumulative precipitation (abscissas) by months, and monthly increment (ordinates) above and below average, for four climatic stations in Ephraim Canyon, 1934–1948.

the other hand, is either Tropical Gulf or Tropical Pacific air masses from south and southwest, or from local convectional storms. Tropical air masses penetrate into central Utah infrequently. Convectional storms are more frequent. The paths of these storms are erratic, and the precipitation-altitude relation of an individual storm, as measured by a single line of gages, is partly a function of direction of storm in addition to orographic uplift. Judging from totals of all storms over a 15-year period, influence of orographic uplift on convectional storms is less than on more general winter storms.

Summary

Precipitation records at four stations, ranging in elevation from 5,543 to 9,860 feet in Ephraim Canyon, on the west front of the Wasatch Plateau, are the basis for this paper. They cover the period 1934 to 1948 inclusive.

Precipitation increases with elevation. The relation between precipitation and elevation is linear, as given by the equation (precipitation in inches, elevation in feet)

$$P = 0.00494\,E - 16.95.$$

A zone of maximum precipitation, formerly believed to occur at intermediate elevations in Ephraim Canyon, is shown to be nonexistent, and is ascribable to concentration of precipitation at Headquarters (8,850 feet) by a high cliff, together with loss of catch at Alpine (10,100 feet) because of windiness.

The yearly pattern of precipitation is that of a sine curve, with a broad crest in late winter (February to April), and broad trough in late summer (July to September). The influence of elevation on precipitation is most marked in winter, least marked in summer. This difference is associated with a difference of storm types, which are predominantly general in winter and local and erratic in occurrence in summer.

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THE USE OF A THERMISTOR IN A STUDY OF SUMMER TEMPERATURE CONDITIONS OF MOUNTAIN LAKE, VIRGINIA[1]

Introduction

Mountain Lake is located in the Appalachian Highlands on the summit of Salt Pond Mountain near Pembroke in Giles County, Virginia. It is a high altitude (4,000′) seepage lake with an area of approximately 100 acres, and a maximum depth of about 100 feet. During the course of some limnological examinations of natural waters in the vicinity of this lake during July and August, 1947 (Shoup '48) a number of general temperature determinations were made from surface to bottom of the lake by means of a Taylor maximum-minimum recording thermometer. These measurements indicated that a midsummer thermocline, with a variation in temperature of at least 15° C, existed between the uniform epilimnion of warmer water and the underlying uniform hypolimnion of colder water. The thermocline or zone of thermal transition in this lake is not very different from that identified in the original studies of this type on Beasley Lake, Wisconsin, in 1898 (Birge '04), and upon other Wisconsin lakes reported upon in 1911 (Birge and Juday '11). In July, 1929, Juday, Birge and Meloche

[1] A contribution from the Mountain Lake Biological Station of the University of Virginia.

('35) found that Big Carr Lake, Wisconsin, a seepage lake of soft water quite similar to that of Mountain Lake, demonstrated a similar temperature relationship with the thermocline confined during July to depths between fifteen and fifty feet.

The measure of success achieved in such studies of water temperature relations in lakes depends to a large extent upon the utility and availability of temperature measuring instruments and the speed and accuracy with which they attain equilibrium for rapid readings. For example, in order to detect possible "microstratification," or the more restricted minute variations of temperature within the three thermal areas of epilimnion, thermocline, and hypolimnion, it is necessary to have a rapid-recording thermometer which may be read without stirring or disturbance of the water. In most lakes, use of either a deep sea reversing thermometer or a Taylor maximum-minimum thermometer would not be advisable for this reason. Thermocouples and platinum resistance elements meet the needs of speed and accuracy, but they have not been used in many instances because of the limitations imposed by high costs for the initial equipment. A critical review of these and other measuring instruments in common use for water thermometry has been given by Welch ('48).

A new type of resistance thermometer, the thermistor (Becker, Green, and Pearson '47), has now been adapted by us for use as a limnological instrument for water thermometry, and we have employed this instrument for detection of summer thermal stratification in Mountain Lake. The chief advantage of the thermistor over either the thermocouple or platinum resistance element is in its marked sensitivity, which permits the use of more rugged and less expensive external indicating equipment. Two additional advantages of a thermistor over a thermocouple are that: (1) its high impedance eliminates for practical purposes resistance problems in circuit design, thus permitting any length lead wires, and (2) there is no need for a junction maintained at a reference temperature. The general uses and methods of thermistors in ecological and physiological temperature investigations have been reviewed by Platt and Wolf ('50). Since an examination of the literature, however, does not indicate prior use of this sensing element in water thermometry, it is desirable to describe its use here and to indicate its general applicability to this type of investigation.

The Thermistor, Method and Use

A Western Electric Thermistor, Model D166382, was selected for water thermometry. In this model the thermistor bead is sealed inside of and supported by a hollow glass bulb, to which heavy lead wires are attached (fig. 1A). The thermistor bead itself is a 0.4 mm diameter glass coated spheroid with two 0.025 mm diameter platinum alloy leads, the latter being soldered to the heavy lead wires embedded in the walls of the glass mount. This thermistor has a temperature coefficient at 25° C of $-3.4\%/C°$, a thermal time constant in still air of 0.1 mw/C°, and a nominal resistance at 25° C of 2,000 ohms.

The associated circuit is the same as that described by Platt and Wolf ('50) for direct contact thermometry, using thermistors D170575 and V597. These thermistor models differ primarily from the one used here in their being naked rather than being housed within a glass bulb. This circuit, based on a Leeds and Northrup single range portable potentiometer, is relatively inexpensive, easily constructed, and will give temperature indications to within 0.01° C. By the use of more sensitive galvanometers a much greater temperature sensitivity is obtainable.

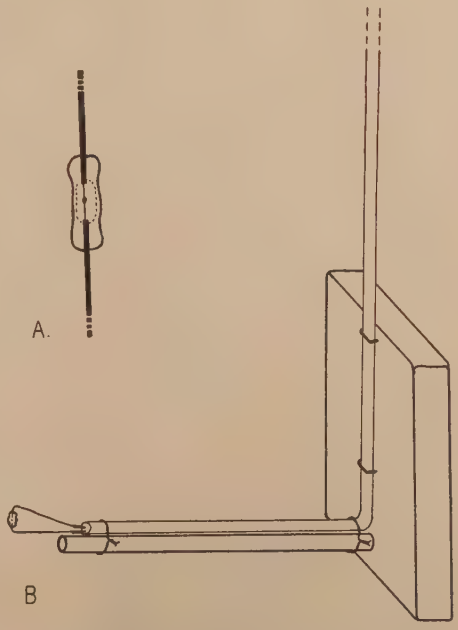

Fig. 1. A. The sensing element. The thermistor bead is sealed in a hollow, cylindrical glass housing, with its delicate lead wires attached to heavy external ones.

B. Attachment of thermistor to lead weight. The end of the lamp cord with thermistor attached is supported by a wooden dowel rod embedded in the weight.

For lake measurements presented here the thermistor was attached to the potentiometer by 150 feet of double strand rubber-covered lamp cord. A five pound lead weight was fastened above the thermistor in such a way that the thermistor was extended five inches horizontally from the weight (fig. 1B). Thus the thermistor was protected from any damage which might occur on striking bottom had it been attached directly below the weight itself. At this distance from the lead weight the thermistor was not influenced by temperature "lag" changes in the mass of the weight itself. The double strand wire was marked at one-foot intervals so that depth could be read directly at any instant.

In making the determinations the boat was securely anchored, and the thermistor gradually lowered, pausing at the designated depth intervals for reading of the resistance values in millivoltages. These values were recorded as rapidly as obtained, and then calculated in degrees Centigrade from the calibration records of the instrument. Due to the construction and sensitivity of the instrument, several precautions had to be taken to avoid small errors. Since the zero of the particular galvanometer used changes slightly when its position is al-

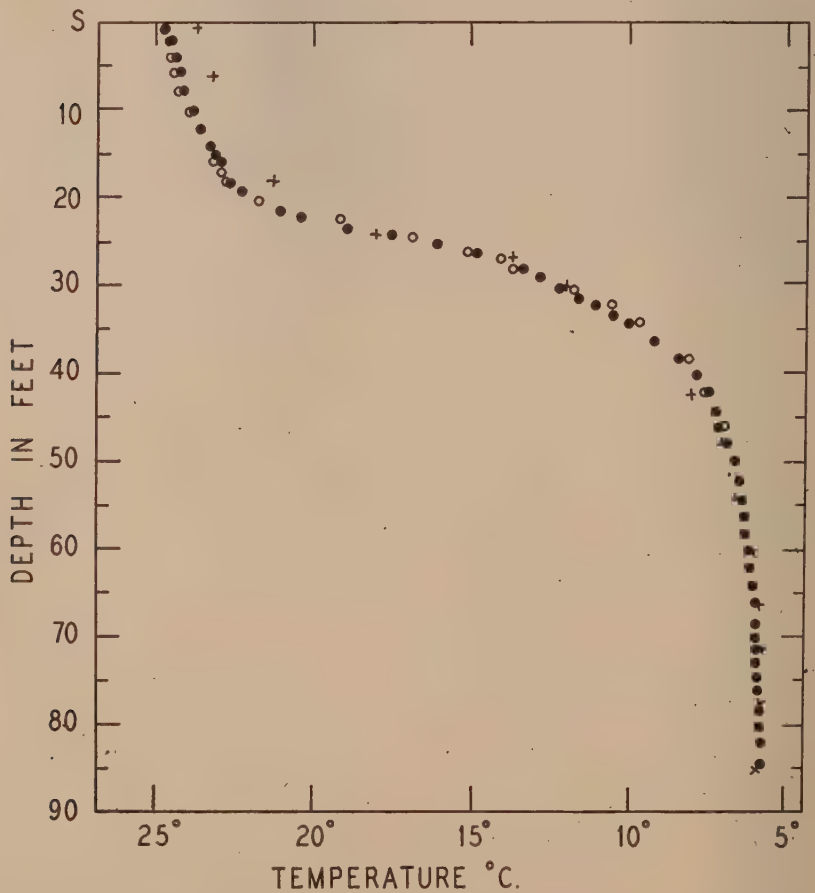

FIG. 2. Temperature relations in the waters of Mountain Lake, Virginia, August 15, 1947, obtained at station of greatest depth. The closed circles represent determinations made on lowering of the thermistor element through undisturbed water, the open circles represent deviations from these obtained on return of the thermistor to the surface, while the crosses represent determinations obtained a few minutes later by use of a Taylor maximum-minimum thermometer.

tered from the horizontal, a level was placed on the instrument case, and readings were made only when the boat was steady. A jerky or rapid lowering or raising of the instrument, with the resultant mixing of the water locally around the element, produces temperature variations which would be sufficient to obscure possible normal micro-fluctuations due to inflow of water from the shoreline areas which might settle at levels in the epilimnion. Best results were obtained when the thermistor was allowed to penetrate undisturbed water. Because of the steeply sloping sides of the lake bottom at the deepest end, the thermocline is not perfectly horizontal over that area. Therefore, with a short horizontal shift of the boat, a minute vertical shifting of the temperature gradient was indicated by a step in the curve. Still another source of error is vertical movement of the boat by wave action. These errors caused by movement of the boat were for the most part avoided by anchoring it, and by restricting its use to calm days. When all such precautions were observed, successive curves obtained at any one station were almost identical, as is shown in figure 2.

Determinations were made with the Taylor maximum-minimum recording thermometer at the same hour and at the same stations by members of the class in limnology of the Mountain Lake Biological Station conducted by one of us (Shoup). This instrument gave less accurate readings and required a time period at least four times greater for top to bottom examination than that needed by the thermistor. We are indebted to the class personnel for furnishing us with the thermometer measurements.

Results and Discussion

These studies of the mid-summer temperature relationships of Mountain Lake were undertaken during the months of July and August, 1947. The lake is fed in part by spring and surface drainage from adjacent heavily wooded regions of sandstone which are of Upper Silurian and Lower Devonian age, and in part by underwater springs arising from the lake basin which is primarily of the Martinsburg shale of the upper Ordovician. The lowest portion of the lake lies in what is probably a partially filled limestone sink and it is through this sink that complete drainage has occurred at least four times during the last 250 years, the last instance of this being in the year 1865.[2]

The waters of Mountain Lake, derived chiefly from the well-wooded and relatively insoluble shales and sandstones, contain a very low quantity of dissolved substances, and in general they are of a derivation similar to that found in high alpine lakes (Hutchinson and Pickford '32). The total alkalinity (bicarbonate) determined at various localities and depths showed that five to eight parts per million (M.O. Alkalinity) were of available buffer. Likewise the lake water carries relatively small amounts of discrete particles in suspension, as indicated by Secci disc readings (table I). From these findings it is evident that any temperature relationships which might involve thermal stratification are not due to concentration of dissolved substances.

Table I. *Secci Disc readings, Mountain Lake, Virginia, August 13, 1947. 3:00 P.M. Bright sunlight. Extinction disc about 8 inches (20 cm) diameter*

Station	Extinction point in ft.
9	21 ft.
2	23 ft.
3	25 ft.
4	21 ft.

Temperature measurements of Mountain Lake in August, 1947, indicated a well-established thermal equilibrium with respect to various depths (fig. 2). In general, from the information we have obtained, the surface waters show some mixing, due to wave action, boating, and some swimming in certain portions of the lake. This mixing is principally confined to the top of the epilimnion and decreases toward the top of the thermocline. The day-to-day temperature studies of the epilimnion will show slight variations not exceeding 2.0° C, which may be of some small influence down to about the 15-foot level. In our measurements of August, 1947, the top of the thermocline may be identified in nearly all determinations at approximately the 20-foot level.

The thermocline, with its extremely marked change in temperature with depth, continues to about the 40-foot level, where it becomes quickly stabilized. From the 50-foot depth on to the bottom of the lake, the temperature drops less than 1° C, settling at 65 feet to a constant reading of 6.00–6.08° C.

Summary

A thermistor has been used as a limnological instrument for measurement of relationships of temperature with depth in Mountain Lake, Virginia, during August, 1947. Its general use and adaptability is indicated.

Stabilized summer conditions of this lake indicate a thermocline at the 20–40-foot level, and uniform temperatures of about 6° C for the 65-foot level, marking the upper limit of a constant hypolimnion.

No thermal microstratification, or small localized deviations of temperature departing from

[2] Private communication from Dean Ivey F. Lewis of the University of Virginia.

the regular temperature curve can be detected, although this new instrument is admirably suited for the detection of slight thermal variations.

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SOME FACTORS AFFECTING FLOWER PRODUCTION IN *ANDROPOGON GERARDI*[1]

Extensive plantings of Big Bluestem Grass (*Andropogon gerardi* Vitman) were made in 1936–38 in the University of Wisconsin Arboretum by means of transplanted wild sods. These plantings grew vigorously but after the first few years failed to produce many flowering stems. It was noticed that those plants which had been subjected to prescribed spring or autumn burns bloomed profusely (Curtis and Partch '48). Subsequent trial confirmed this effect of fire. Similar results have been reported for several southern grasses by Burton ('44). In the case of the Big Bluestem it was thought that the fire could act in one of three ways: One, by direct effect of the heat of the fire on the buds in the plant crown; two, by removal of the accumulated litter from the previous years' growths; or three, by liberation of mineral fertilizers from the ashes. The present paper presents the results of an experiment designed to explore these three possibilities.

Replicated plots of such size as to include at least 10 of the originally planted clumps were set up in randomized blocks in previously unburned areas where the grass showed optimum growth. The six plots in each block received the following treatments: 1. The old litter was removed by fire in mid-March, 1949 (the ashes were not disturbed); 2. As no. 1, but the ashes were carefully removed by sweeping immediately after the fire; 3. As no. 2, but the plot was re-covered by the litter obtained from no. 4 in manner which simulated the natural cover as closely as possible; 4. The old litter was removed by careful hand-clipping at a height comparable to that remaining after the fire in no. 1; 5. As no. 4, but the ashes from both no. 2 and 3 were scattered on the plot after it had been clipped; 6. Control plot with no treatment. Observations were made at the peak of the blooming season in late summer. Measurements included basal area per clump, average height of the flowering stems, and number of flowering stems per clump.

The results, in the form of averages, are shown in table I. Flower production is presented in terms of number of flowering stems per square inch of basal area, thus compensating for differences resulting from clumps of different size. The effects of cover removal and fertilization for treatments 1, 2, 4 and 5 were separated by use of an analysis of variance. The effect of all treatments was studied by means of individual comparisons with the control values, using the *t*-test of significance. The results of the individual comparisons are shown in table I where the asterisks indicate values which are significantly different from the

[1] Contribution from the University of Wisconsin Arboretum. Journal Paper No. 16. This grass was formerly called *Andropogon furcatus* Muhl.

TABLE I. *Effect of fire, clipping and fertilization on* Andropogon gerardi; *averages of four replicates of ten clumps each*

Treatment	Flowering stems per sq. in. of basal area	Basal area per clump	Ave. height of flowering stems
1. Burned only	0.253*	376 sq. in.	72.8 in.*
2. Burned and swept	0.210*	348	74.5 *
3. Burned, swept and covered	0.087	293	46.7
4. Clipped only	0.185*	309	71.9 *
5. Clipped plus ashes from no. 2 and no. 3	0.203*	336	73.0 *
6. Control	0.036	291	46.0

* Significantly different from control (1% significance level by *t*-test).

control at the 1% level. The analysis of variance showed that the addition of fertilizer in the form of ashes gave more flowers (significant at 5% level) on both burned and clipped plots, while burning was better than clipping (significant at 5% level). The average height of the flowering stems was increased in all cover removal plots, but the method of removal was not important. The basal area per clump was not significantly affected by any of the treatments. In no case did the plots which were burned, swept and covered differ significantly from the control.

These results indicate that the most important factor affecting the flowering of *Andropogon gerardi* under the conditions of this experiment was the presence of a cover of old litter on the crowns. Removal of this cover by either fire or clipping brought about a six-fold increase in flower production and a 60% increase in plant height. The fertilizing action of the ashes remaining from the burned litter was responsible for a small further increase in flower production but it had no effect on plant height. The direct heat of the fire, as isolated in treatment no. 3 where the plants were burned and then re-covered, was insufficient to bring about flowering, but its action cannot be completely ignored, since the burning treatments were better than the clipping treatments.

These conclusions are supported by many field observations in the remnant prairies of southwestern Wisconsin. *Andropogon gerardi* flowers regularly along roadsides and railroad right-of-way, where the ground is "kept clean" by burning every spring. In those few prairies where burning is not practiced, however, flowering is largely confined to isolated clumps and is not general in the areas where the plants form dense stands. In the case of isolated clumps, it appears that the old stems of a given year tend to fall in a radiating fashion about the clump, thus permitting the center of the crown to receive direct sunlight, which in turn allows growth to begin early in the spring. In dense stands, the old stems fall in a similar pattern, but the crown of any one plant is covered by the stems of its neighbors. In such cases, the growth is delayed in the spring for as much as three or four weeks. It is possible that the fire and clipping treatments in the present experiment exerted their positive action on flower production through the simple removal of the insulating blanket of old stems, thus permitting the plants to begin growth early and to build up a favorable carbohydrate reserve before the normal period of flower primordium initiation.

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CAN TRADITIONAL ECOLOGY EMBRACE HUMAN ECOLOGY? A LETTER TO THE EDITORS

Dear Editors,

I was very much interested to learn that the Ecological Society of America at its meeting in December, 1949, passed a resolution urging the study of the application of the methodology of ecology to human ecology in UNESCO and offered the services of the Society to implement the resolution.

Certainly in these times we cannot afford to overlook any shred of knowledge or body of theory which could conceivably be applied to help direct human interaction into more constructive channels. However, does this also imply extension of traditional ecology into a sort of universal ecology embracing the whole human interaction complex? If so, there will

be serious obstacles encountered, some of which will be purely scientific ones, which should be recognized early and resolved at the scientific level before they are transferred to the emotional level where they will become largely unsolvable. With this in mind, may I as neither social scientist nor ecologist suggest some of the scientific obstacles that can be expected if an attempt is made to blend disciplines dealing with phenomena as different as human and traditional ecology.

New disciplines arise as we concentrate increasing attention on a restricted group of phenomena and create theoretical structures to explain them. As disciplines deepen in the process of developing their concepts concerning the nature of what their adherents observe, they also broaden and impinge upon each other at the level of observation. (There are after all a finite number of phenomena to be observed but an infinite number of ways of looking at them.) In the process of impinging and even overlapping, members of each discipline can communicate ideas, be compatible, or even occasionally come together under one banner only when certain conditions exist. First among these is a similarity in the theoretical structures whereby they explain what they observe. With these similar theoretical structures a broad group of phenomena may be embraced in one discipline such as genetics which runs the gamut of the animate world, including humans. Another example is cybernetics, a relative newcomer which gives some promise of producing theory which can explain certain phenomena occurring throughout both the animate and inanimate world. Without these similar theoretical structures, however, two disciplines may be quite incompatible when dealing with the same phenomena, e.g., psychiatry and some schools of psychology with regard to human behavior.

The basic question then is, are the theoretical structures of plant and animal ecology broad enough to encompass the human complex? With no reflection whatsoever on the adequacy of ecological concepts for explaining plant and animal phenomena, I believe the answer to the question is inherently a negative one. First of all, the ecology of the human presents a far more complex environmental pattern. This pattern is made up of the physical environment in the plant and animal ecology sense plus the cultural environment controlled by the social structure in which the individual lives. This cultural environment appears to exert an effect analogous to but often outweighing the physical environment, but is hardly describable in the same dimensions as the physical environment. A second imposing difference between traditional ecology and the human-environment complex is in the mechanism by which the environment and the organism react. The human organism equipped with both memory and foresight introduces into the picture a host of latent and anticipatory reactions which are quite incomprehensible in terms of ordinary organism-response theory. Finally, and perhaps the most important difference between the two is the level at which the controlling reactions take place. The predominant forces of the human environment are increasingly those emanating from other humans and are at the psychological rather than at the physical level. These phenomena have no counterpart at the plant and animal level. Neither will the principles applicable to the effect of the physical environment, so basic in plant and animal ecology, explain what is being found in the realm of human interaction at the psychological level.

Broad and helpful analogies may certainly be found in extending to human phenomena those theories designed for phenomena at the plant and animal level. Le Compte du Nouy's "Human Destiny" is an excellent example. However, interpolations within these broad analogies or extrapolations beyond them are full of pitfalls and give rise to dangerous over-simplifications, as the application of his generalizations to the education of children so abundantly illustrates. On the other hand, the more elaborate and at present less precise theoretical structures necessary to explain human interaction are apt to annoy, by both their looseness and complexity, those used to more specific and simple theory. The differences in both complexity and preciseness characterizing disciplines at different evolutionary stages may well raise questions concerning differences in scientific standards. The study of human interactions is definitely younger, less precise, and has less well developed theoretical structures than traditional ecology.

In brief, to achieve the requisite degree of similarity in theoretical structures to establish an all-embracive ecology would require extensive and perhaps distressing modifications and extensions of plant and animal ecological theory: first in the area of providing for the powerful influence of cultural factors; second, in providing for new and as yet little understood mechanisms of reaction associated with man's peculiar possession of memory and foresight; and finally, to provide for the often controlling inter-organism reactions at the psychological level.

While such a cosmopolitan extension of a promising discipline is intriguing to consider, it is also probably premature. The "Science of Man" will eventually emerge from the process of putting him and his environment back together, but more likely through the development of a new and far more embracive theory than can arise by a simple extension of any now

available. In the meantime there should be every attempt to push ahead, but with full recognition of the dangerous over-simplifications which arise from extending theory developed to explain one set of phenomena to another set of far greater complexity. Large scale applications of this technique have already occurred with tragic results in the very recent past and with perhaps more tragic ones yet to come.

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BOOK REVIEWS

The Grasslands of Latin America [1]

This latest work in the well-known series by the Commonwealth (formerly "Imperial") Bureau of Pastures and Field Crops is a worthy member of its line. In it is reviewed the literature on the grasslands and related vegetation of the whole Latin American region, including Mexico, Central America and Cuba as well as South America. The magnitude of the task is indicated in part by the length of the reference list, which includes over eight hundred titles, written in a variety of languages. The result is a work of unparalleled reference value, though by no means in the "handy guide" category. As R. O. Whyte states in the preface, "Any reader who expects a short, tidy account of a subject of such magnitude is expecting too much." If the treatment at times seems rambling and the views of the authorities at odds, the reason appears to be the present state of knowledge of the region rather than any fault of the reviewer-author. As in most areas where botanical studies have been limited, taxonomic studies have, so far, outnumbered the ecological. The present lack of detailed ecological information is evident throughout, and in many cases the data quoted are of the most preliminary sort. No doubt a comparable treatment of the grasslands of North America attempted three or four decades ago would have suffered from many of the same defects.

The brief introduction includes useful maps of the climatic regions and soil zones of South America and a highly generalized map of the principal types of plant cover. There follow five chapters dealing with the main groups of grasslands, classified on a basis which is partly ecological, partly economic. The remaining seven chapters cover a variety of topics, including browse and poisonous plant species; soil erosion and conservation; and the organization of botanical and pasture research in the region.

The volume is packed with items of ecologic interest. A prominent feature is the evidence given of rapid and marked changes in the native vegetation produced by domestic livestock. Most of these communities apparently evolved without any such pressure of large native herbivores as was exerted by the bison in North America. As a result, many of the grasslands have been altered drastically, even by rather moderate grazing use. The extensive replacement of indigenous by exotic species invites comparison with the situation in island floras such as those of Hawaii and New Zealand, where a similar process has occurred. On the "moist pampa" of the Argentine, for instance, Parodi lists a total of 488 species, of which 170 are introduced. Some of the common exotics in this and other communities include *Bromus mollis, Poa pratensis, Briza minor, Medicago denticulata* and *Eradium cicutarium,* all well known as introductions in North America. In many instances the introduced species are rated above most of the native plants for grazing value.

The presence of grasslands in many humid or sub-humid regions of Latin America poses interesting ecological problems. Some of the tall grass "savannas," as in the Amazon basin, are obviously subclimax communities maintained by repeated burning. In other cases, grasses appear to constitute a climax. "Unfavorable soil conditions" is given by Parodi and others as the reason for the lack of trees on the "moist pampa" of Argentina. In the vast "llanos" of Venezuela and Colombia, annual flooding alternating with seasonal drought and severe winds creates conditions apparently more favorable for tallgrass prairie than for forest or shrub communities. Numerous references to burning, as either past or current practice, suggest the far-reaching influence of fire in Latin America, and it appears that the effects on native vegetation have not yet been fully evaluated.

Evidence is given of considerable depletion of soil and grazing resources by unwise use. This damage is most pronounced in areas such as Central Argentina, and parts of Uruguay, Chile, and Mexico where grazing use has been most intensive and prolonged. Overgrazing, indiscriminate burning and cultivation of lands unsuited for crop production have all been contributing factors in this process. Frequent references to lowered soil fertility indicate that this is a serious problem on many grasslands, even where erosion has not been abnormal. On the brighter side is the description of the energetic attacks being made on land use problems in many of the Latin American countries.

The volume is well-indexed and contains an extensive bibliography. There are good photos of grassland types in the Argentine, Uruguay and Venezuela. Illustrations of other major communities would have added to the value of the text. Altogether the volume represents a great contribution to grassland ecology and should be a standard reference for ecologists, land managers and others interested in the natural resources of Latin America.

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[1] **Roseveare, G. M.** 1948. The grasslands of Latin America. Bull. 36, Imperial Bureau of Pastures and Field Crops, Aberystwyth, Great Britain. Pp. 1–291, 9 plates, 15 text figs. Price—20 shillings.

Vole Populations [1]

The Levant Vole (*Microtus guentheri* D. et A.) has been a faithful nibbler at the edges of human affairs in the Middle East. The vengeful hand of the Lord on one occasion (Samuel, I: 4) chose the form of a mouse plague in which to manifest itself against the Philistines, who had seized from the Hebrews the sacred ark; the depredations of these small agents of divine wrath must have been no less effective than those of their modern descendants, for the ark was promptly restored along with an additional peace-offering of five golden mice, whereupon the plague abated. Whether or not a result of the decline in the art of goldsmithy, the problem of vole multiplication has remained one of pre-eminence in the development of the agriculture not only of Israel and Palestine, but of Syria, Lebanon, Transjordan and the Turkish Republic. This publication is a summary of the investigations carried out by Professor Bodenheimer and several colleagues since 1929 on many phases of the ecology, physiology and population dynamics of *M. guentheri;* it is considered by its author to be a progress report only, standing for the present in place of a promised monographic treatment of the species.

Like other writers (Elton, Errington) on cyclic mammals, Bodenheimer has concluded that the secrets of vole fluctuations will not be elucidated with refinement of the measurements of physical ecology, which proved more useful in interpreting the irruptive behavior of the Desert Locust (*Schistocerca gregaria*), or, for that matter, from further elaboration of the classical formulations of predator-prey interactions.

It is certainly true that these generalizations, convenient as they may be, have overlooked some of the most suggestive data. It has been observed in certain cyclic birds as well as mammals that the apparent fertility can change greatly with the stage of its cycle, and it might be suggested that cyclic organisms have the additional character of a rather peculiar reproductive plasticity. Such innate traits are really antecedent to the more prominent *effects* like disturbance in the rate of predation.

It now appears quite appropriate to say that the magnitude of the environmental stimulants related to the cycle may be of an order much more subtle than one had heretofore insisted upon. It has been impossible, probably, for the author to examine some recent interesting papers by Siivonen, and particularly one by P. Palmgren, who has suggested that the proper additive combination of several randomly fluctuating time series may produce a pseudo-cycle of quite reasonable regularity. Thus the pseudo-cyclic recurrence of certain combinations of randomly fluctuating ecological variables (undetectible by the investigator working with only one or a few) would be able to multiply its effect by provoking a chain-reaction within the unstable population physiology, which would then run its own course quite independently of major changes in the "environment" of the physical ecologist. The instability of a self-regulating mechanism like an animal population does not necessarily proceed from instabilities in an external source of energy; the structure of the system itself is of quite as much importance.

Bodenheimer has investigated the bases for such instability in some detail. From laboratory data on "physiological" longevity and reproductive capacity, the customary Malthusian and stable-stationary life-tables have been constructed. Though the differences between these are profound, they are apparently no greater than the differences between irrupting and quiescent vole populations in nature. It is impossible to draw any useful conclusions from this, however, until more field data than the author has at his disposal are available. The manipulation of synthetic life-tables is not a *ne plus ultra.* A comparison was made between the stable-stationary age-distribution thus obtained and the age structure of a quiescent population estimated from weights of the lower jaws in pellets of the Barn Owl (*Tyto alba*) which preys locally on the vole. The agreement was good, though this is an objectionable census method, and only ages in excess of 25 days, when the voles become accessible to the owl, could be recorded. The vital information on natural age structure during peak years appears to be lacking.

The hormonal and other determinants of apparent fertility are discussed at some length. Following the interesting observation that the vole shows similarities in reproductive physiology to the rabbit (ovulation proceeds only as part of a copulatory reflex pattern), Bodenheimer suggests that there may be other similarities, particularly with regard to the ability of diet to regulate apparent fertility. Foods (alfalfa meal) having a (neurotoxic) gonadotropho-mimetic effect in the rabbit were found to be without any striking effect on litter size in the vole, although this and the proportion of successful impregnations could be increased by factors of 1.3–1.8 by feeding or injection of mammalian gonadotrophic preparations. Such artificially produced reproductive characteristics resemble very closely those which appear in the

[1] **Bodenheimer, F. S.** (Dept. of Zoology, The Hebrew University, Jerusalem). Problems of Vole populations in the Middle East: Report on the population dynamics of the Levant Vole. Publ. by The Research Council of Israel, Jerusalem, 1949. 250 Mils (5 s.). Pp. 1–77.

wild population at the onset of a peak (litter size increasing from 3–8 to 6–14, and an increased proportion of pregnant females). It is to be hoped that comparisons may be made eventually in the details of reproductive physiology with other closely related and sympatric forms which have not been involved in irruptions as spectacular as those of *M. guentheri* (*M. nivalis, Arvicola amphibius*).

The final chapters are of more local interest, and recount the statistics of vole damage under specific types of agronomic practice, and to particular crops, as well as surveying various practical methods of control. Of the latter, the most widely used at the present time is baiting with thallium sulfate-treated grain. The total biological significance of the element thallium is extremely obscure, and has thus far been treated for the most part as an *ad hoc* problem in microtine toxicology, with due respect to some of its effects on certain domestic animals and man. The position of thallium in the periodic table suggests that it may adhere very closely to localities where it is used as a muricide; thus the effects, beneficial or otherwise, of the accumulation of thallium in agricultural soil may provide the future middle-eastern vole expert with an interesting biogeochemical interlude to occupy him during unexciting parts of the cycle.

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THE ORIGIN OF LIFE[1]

This is a rather hererodox, quite heretical book, if viewed from the standpoint of modern evolutionary thought. Much of what we consider well founded and supported, so that it serves as the base for our evolutionary views, is attacked and rejected by Plaumann. Many ideas intended to replace the rejected ones are offered. Thus this book shakes at the very foundations of our generally accepted biological ideology; it therefore should be taken seriously and studied, even if the reasoning against evolution convinces us as little as do the new ideas of the origin of life in general presented in this work. The author is a well known and appreciated field entomologist who has spent many years in the virgin forests of Brazil, collecting, observing and studying directly from nature. He resents the estrangement from nature of modern biologists, and the supersession of field work by closet work, a tendency really existing in our times that threatens to grow into a serious obstacle to biological research, at least in the original meaning of the term "biology."

We cannot follow Mr. Plaumann in his anti-evolutionistic ideas and in his theory of the origin of life from "primitive germs" (Urkeime), which reached earth from space at the ends of the various geological epochs, with a new "creation" on each occasion; neither can we accept his rejections or his substitute ideas, for which he fails to give sound reasons. We have to be thankful to the author, however, for having exposed certain weak spots in current evolutionary reasoning, of which we all know, and for his justified campaign to lead biology and biological studies from laboratory and writing-desk back to living nature.

[1] **Plaumann, Fritz.** Die Entstehung des Lebens. Völlig neue Anschauungen über die Entstehung des Lebens und der Menschen. Rotermund & Co., São Leopoldo, Rio Grande do Sul, Brazil. Pp. xii + 379. $7.50.

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SEA TURTLES[1]

This book is a brief summary of the known facts about the marine turtles of the Caribbean region. All phases of this subject including taxonomy, distribution, growth, and general ecology are dealt with. In addition commercial aspects are also considered, and some attention is given to the possibility of turtle culture.

An annotated bibliography is included, and this is presented in such a manner that the worker can at a glance see what references are of importance to him. The need for such a bibliography has been obvious to all workers in this field, for the literature on marine turtles is scattered in a vast number of publications, many of which could be easily overlooked or are extremely difficult to obtain. The bibliog-

[1] **Ingle, Robert M., and Walton Smith, F. G.** Sea turtles and the turtle industry of the West Indies, Florida and the Gulf of Mexico, with Annotated Bibliography. University of Miami Press, 1949. A Special Publication of The Marine Laboratory, University of Miami, in cooperation with The Caribbean Research Council. Pp. 1–107. $1.00.

raphy has been compiled with care. Considering the scattered nature of the publications it is not surprising that some rather important references have been overlooked (e.g., C. Bernard Lewis—The Herpetology of the Cayman Islands). There are minor defects in this publication, such as the confusion created by the use of different scientific names for the same species. One feels that, particularly for the lay reader, better figures with fuller naming of parts would have been desirable. The growth rates quoted are derived from experimental data and appear much lower than had usually been supposed.

This work does not attempt to be original research; it is intended as a ready reference on the present state of our knowledge. In considering our present knowledge certain obvious gaps appear. What is the relationship between lunar periodicity and the breeding cycle? What is the age at maturity? Are there local races of turtles recognizable in different localities or do the adults migrate extensively over the area? In connection with the last point, evidence from commercial fishermen on the hawksbill turtle is completely contradictory. This latter point is of importance in considering conservation and artificial propagation methods.

The great value of this book and its future usefulness reemphasizes the need throughout the Caribbean area for summarization of data on the marine resources. It should emphasize the extremely valuable work which the Marine Laboratory of the University of Miami is doing for the whole area. This laboratory is now unquestionably the preeminent center of marine research for the West Indies, and workers engaged in this field would be well advised to consult with its director.

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ERRATUM

In the paper by Syunro Utida, "On the equilibrium state of the interacting population of an insect and its parasite," published in *Ecology*, Volume 31, Number 2, Table II (p. 168) is erroneous. The body of the table should stand as follows:

	Population A	Population B
Initial density of the hosts	3.24	3.15
Final density of the hosts	2.34	2.92
Density of the parasites	3.18	3.12